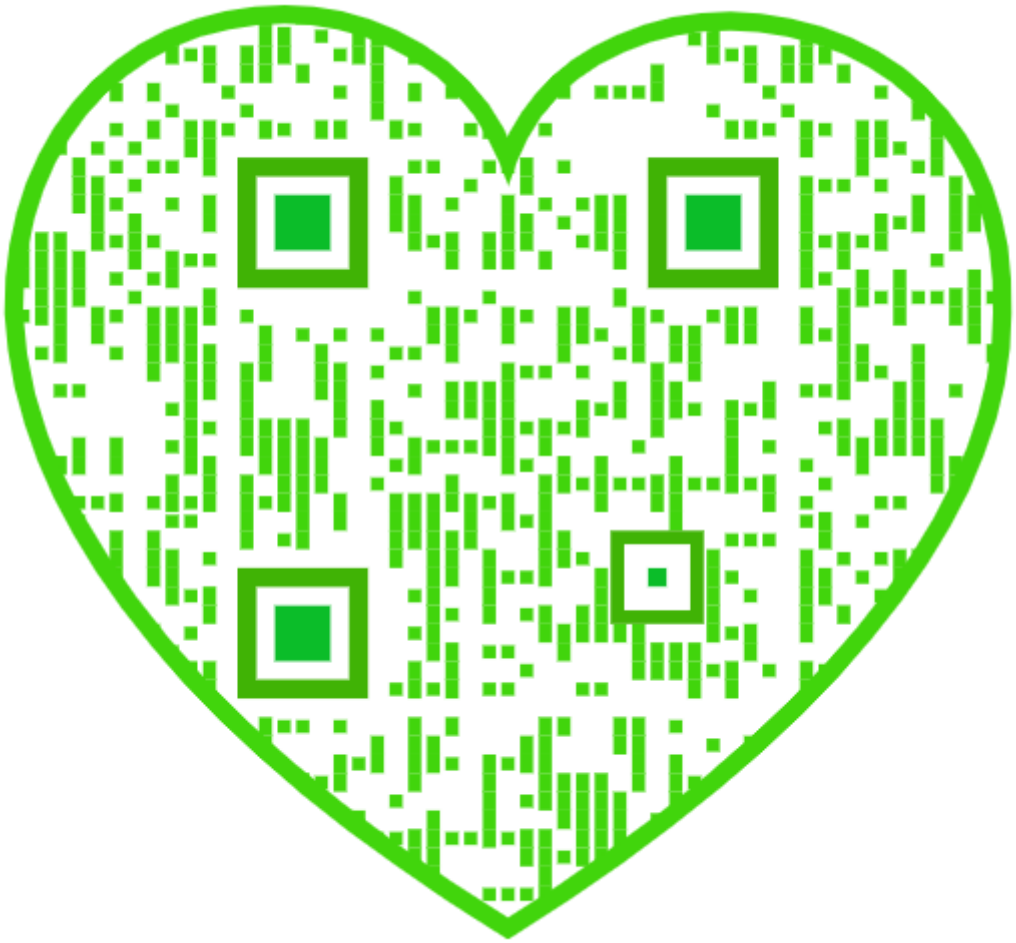

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The Comparative Anatomy and Phylogeny of the Cyperaceae[1].

BY

AMON B. PLOWMAN.

With Plates I and II and two Figures.

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[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 2.

[Annals of Botany, Vol. XX. No. LXXVII. January, 1906.]

INTRODUCTION.

SINCE the publication of De Bary's (12) great work on Comparative Anatomy, and Van Tieghem's (57) subsequent 'stelar theories,' there has accumulated a considerable body of literature devoted to this phase of botanical study. The work of De Bary marked the culmination of that earlier mode of treatment which considered the axis of vascular plants to be made up of more or less numerous, wholly independent fibro-vascular bundles, embedded in a common matrix of fundamental tissue. Van Tieghem (57) later introduced the idea of a fundamental stelar unity of the fibro-vascular system, and showed that this unity held essentially true of all the Vasculares. The elaboration of this view lent new interest and broader possibilities to the anatomical study of plants; and while many of the details and assumptions of Van Tieghem's theory have been disproved or modified by the later investigations of Gwynne-Vaughan (20), Jeffrey (27), Boodle (4), Faull (18), Worsdell (61), Schoute (45), Chrysler (9), and others (5, 17, 21), yet the important fact still remains that in the fibro-vascular system of higher plants we find an essential unity of plan which is fairly comparable to that found in the skeletal system of vertebrate animals, and which is apparently of hardly less importance from the phylogenetic point of view.

In the hope of gaining some new light upon the vexed question of the relationships of the Monocotyledons, the writer has undertaken the present study of the Cyperaceae, a group which is especially interesting on account of its apparently somewhat isolated position and its clearly-marked characters.

Upon making a general survey of the problem before us, the following questions, among others, present themselves for careful consideration, if not, indeed, for solution :—

1. Anatomically considered, do the Cyperaceae constitute a clearly-defined group?

2. What subdivisions of the Cyperaceae may be made upon the basis of anatomical characters?

3. Of what importance are oecological factors in determining the anatomical features of the group?

4. What is the nature, origin, distribution, and significance of the amphivasal bundles found in this group?

5. What is the course of the fibro-vascular bundles through the stem?

6. Of what importance are leaves as factors in stelar development?

7. What structural characters of the Cyperaceae are ancestral, and what are more recently acquired?

8. What are the probable phylogenetic inter-relationships of the Cyperaceae?

9. What is the position of the Cyperaceae among the Monocotyledons?

10. What bearing have the observed facts upon the phylogeny of the Monocotyledons as a whole?

Before entering upon a discussion of these problems it will be necessary to consider in more or less detail some of the structural characteristics of representative genera and species of the Order.

The Root.

The internal structure of the root in the Cyperaceae presents a striking degree of uniformity. The central cylinder is compact and relatively small, surrounded by a well-marked endodermal sheath, the cells of which commonly have the inner wall much thickened. The medulla is composed of round, more or less sclerotic cells of relatively small size, with sharply-defined intercellular spaces. The xylem masses are radially disposed within the bundle-sheath, alternating with the phloem masses. Their number is variable, but rather smaller than that found in the majority of Monocotyledons, ranging from six to eight in species of *Eleocharis* to fifteen to eighteen in certain Carices, while, according to Kny (32), these numbers may approach or even exceed 100 in the roots of some Palmales. Each xylem-mass consists of a few short, small, thin-walled tracheids arranged in a radial plate terminated centrally in a single relatively large vessel. It frequently happens that there are not as many large vessels as there are xylem-masses, in which case growth pressure may cause a vessel to lie at the point of a V of which the arms are two distinct xylem-masses, which are brought in this way to subtend the intervening phloem-mass, in a manner remotely suggestive of the collateral arrangement of the elements found in the stem. It is worthy of note that, as shown by Klinge (31), the elements of the protoxylem are as a rule neither spiral nor annular, but scalariform, reticulate or pitted.

The phloem is less conspicuously developed, the masses being quite small and often but slightly differentiated. In mature roots the elements are either partially lignified or considerably crushed by growth pressure. It has been shown by Chauvaud (8) that the sieve-tubes are derived in each case from a 'pericambial' cell lying next to the endodermis. The phloem is separated from the xylem by a few or sometimes numerous rows of usually somewhat sclerotic parenchyma-cells.

The cortex of the young root consists of many layers of thin-walled cells arranged with great regularity in radial rows. In mature roots this regularity of structure is usually wanting, owing to the presence of large air-chambers in the cortex, separated by very thin radial plates of cells. This feature is especially conspicuous in sedges of aquatic or limicolous habit. The piliferous layer is not specially modified, and is usually

strengthened by a narrow hypodermal zone of more or less sclerotic mechanical tissue. Tannin-sacs are of quite common occurrence in all parts of the root.

The primary root arises from the micropylar end of the protocaulome. It is of relatively short duration and little importance. Secondary roots arise endogenously from the rhizome. Rootlets are derived from the rhizogenous pericambium situated just within the endodermal sheath. It is a well-known fact that in the Gramineae this pericambial sheath is interrupted at the xylem plates, which lie in actual contact with the endodermis. The earlier investigators believed the grasses to be altogether unique in this respect, all other Monocotyledons as far as studied showing a continuous rhizogenous zone. An uninterrupted pericambium has been demonstrated by Van Tieghem (54) in species of *Carex* and *Cyperus*, and more recently by Holm (25) in *Carex Fraseri*. However, later studies by Van Tieghem and Douliot (58), De Bary (12), and Klinge (31), reveal the interesting fact that the majority of the Cyperaceae resemble the Gramineae in the possession of an interrupted rhizogenous pericambium, while a few species have a uniform, continuous pericambial sheath, and still other species show various stages intermediate between these two conditions. Consequently there are two types of origin of rootlets. In the majority of cases, where the rhizogenous zone is interrupted by the smaller xylem-elements, the rootlet is inserted opposite a phloem-strand, and the xylem-elements are derived from the two adjacent xylem-strands, so that the oval base of origin of the rootlet has its longer axis transverse to the main axis of the parent root. On the other hand, in those cases in which the pericambium is continuous the rootlets are inserted directly upon the xylem-strands, each rootlet connected with but a single strand, and having the longer axis of its oval base of attachment parallel to the main axis of the parent root.

These facts have a certain interest from their bearing upon the relationships of grasses and sedges as expressed by Van Tieghem (56) and others, and to be considered more fully on a subsequent page. In its apical development the root presents no features uncommon to the great majority of the Monocotyledons. As shown by De Bary (12), Van Tieghem (56), Treub (53), and others, the root-cap is developed from a distinct calyptrogenic initial meristem, outside and independent of the dermatogen, so that the piliferous layer presents a smooth contour, traceable under the root-cap quite to the initial region.

The Rhizome.

The great majority of the Cyperaceae grow by a perennial root-stock, which is in some cases long and slender, in other cases extremely short and compact, while other members of the Order present all intermediate

conditions. Even the annual species commonly preserve the rhizomatous habit, the first few internodes of the stem being very short and usually growing more or less obliquely in the soil. Indeed, where the rhizomatous character of the stem-base is not apparent externally, it is always demonstrable from internal structure.

Frequently the rhizome bears hard, brown leaves of considerable size at the nodes, but more generally the leaves are reduced to mere scales. After a period of horizontal or oblique growth the rhizome bifurcates to give rise to an aerial stem or culm which is commonly leafy, at least at the base, and which ultimately bears the inflorescence. Not infrequently several aerial axes are given off from the rhizome in a single season's growth, some of them being only vegetative, while others bear both leaves and flowers. But it more often happens that the number of aerial shoots is very small in each season's growth, and all of them ultimately develop flowers. Fibrous roots are produced in large numbers from the nodes of the rhizome. In most cases the elongated rhizomes are not of uniform size throughout their length, but consist of swollen nodes and slender internodes, as in *Scirpus americanus*; or the rhizome may be made up of swollen tuberous portions connected by slender internodes, as in *Cyperus esculentus*, and to a less marked degree in *Scirpus cyperinus*, *S. atrovirens*, *S. lineatus*, &c.; only rarely does one find the rhizome of uniform size for a considerable part or the whole of its length, as in *Scirpus robustus* and a few of the Carices.

Internally the rhizome consists of a central cylinder which is very rarely hollow in the mature condition, as in *Carex scoparia*, *Cladium mariscoides*, *Dulichium arundinaceum*, &c., but which as a rule is solid or only slightly aerenchymatous, and composed of several to very many fibro-vascular bundles embedded in fundamental tissue and surrounded by a well-defined endodermal sheath (except in *Scirpus microcarpus* and *Cladium mariscoides*), which is either simple or variously reinforced by circular fibres or a sclerotic zone. Outside the endodermis is the very variable cortex, bounded externally by the epiderm. The cortex may be sclerotic in whole or in part, unmodified parenchyma, aerenchymatous in varying degree, or even cavernous as in the upper side of the rhizome of *Dulichium*. Bordet (6), Palla (35), and others have attempted to utilize the characters of the cortex as diagnostic features of the Cyperaceae, but with very doubtful success, owing to the fact that these features are extremely variable under change of environment. The peripheral portion of the cortex is very generally modified to form a sclerotic hypodermal zone, or at least a series of hypodermal ribs, of which the function is clearly mechanical. The epidermis is not infrequently sclerotic, and rarely covered with a thick cuticle. Tannin-sacs are of common occurrence throughout most rhizomes. With a few rare exceptions among the Carices, starch is everywhere present

in the rhizome of the Cyperaceae. It is found in especially great quantities in *Scirpus robustus* and *S. americanus*, and in the tuberous rhizomes of many species of *Cyperus*.

It has been found that outside the central cylinder all of the characters are more or less highly susceptible to the influence of environment, often presenting a considerable range of variation within the same species, and consequently possessing comparatively little value from a phylogenetic point of view. Accordingly our attention will be directed more specifically toward the characters of the central cylinder itself.

In the seedlings of *Scirpus microcarpus* the central cylinder presents a condition of affairs strikingly similar to that described and figured by Chrysler (9) for *Smilacina*, the only difference being found in the somewhat more numerous leaf-gaps and in the earlier appearance of numerous medullary strands, which, however, are almost without exception of the collateral type. Young plants of other species indicate a similar tubular condition of the central cylinder in its earlier stages, followed in later development by the appearance of medullary strands, which in the majority of the Cyperaceae are of the concentric type. Thus it appears from a cursory glance at the seedling of the Cyperaceae that the central cylinder in its earliest stages is a simple siphonostele of the phyllosiphonic type, similar in every essential particular to that of the Dicotyledons. Only in later stages of growth does one find a highly complicated arrangement of stelar structure. It seems very desirable that the developmental history of the Cyperaceae should be more thoroughly studied.

The central cylinder of the mature rhizome may be described under two fairly well-marked general types, which are characterized by the disposition of the xylem-elements of the fibro-vascular bundles. In the first of these types, which is by far the more common among the Cyperaceae, all or most of the bundles are of the concentric sort, with the xylem distributed more or less uniformly all around the phloem. To such bundles the term 'amphivasal' has been very generally applied, and those Cyperaceae which present this type of rhizome bundle may, for purposes of description, be grouped together as the Amphivasae. Here belong most species of *Scirpus*, *Cyperus*, *Eleocharis*, *Eriophorum*, *Rhynchospora*, and *Carex*. In certain other forms, notably *Dulichium*, *Cladium*, *Scirpus microcarpus*, *S. americanus*, *S. robustus*, &c., the bundles are of the simple collateral type, with the relatively few xylem-elements disposed on the centripetal side of the bundle. Those forms which present this arrangement may be termed the Centrivasae.

Scirpus cyperinus will serve as an example of the Amphivasae. A part of the central cylinder of this species is shown in Pl. I, Fig. 3, and a part more highly magnified in Fig. 4. It will be observed that the bundles are very numerous and almost exclusively of the amphivasal

type. The majority of them are grouped near the peripheral portion of the central cylinder, while each of those lying nearer the centre is characterized by the possession of a large centripetal mass of sclerenchymatous tissue. This is the greatly exaggerated peridesm of the bundle, which in the peripheral bundles is either more uniformly distributed or even wholly undifferentiated.

The phloem-mass is composed of very numerous, small, thin-walled elements of fairly uniform size, not readily distinguishable as sieve-tubes and companion-cells. However, in closely related species of less compact habit of growth, such as *S. atrovirens* and *S. sylvaticus*, it is often possible to make out these different elements of the phloem quite definitely. The xylem-elements are rather small but of various sizes, crowded in a dense ring around the phloem. Often there may be more than a single ring of xylem, or an irregular massing on one side. In some of the bundles, particularly those lying centrally, there is a small but unmistakable protoxylem-lacuna on the central margin. This is an indication of the original collateral nature of these bundles. As Chrysler (9) and other observers have shown from developmental studies, amphivasal bundles are derived from collateral bundles by excessive development of the xylem elements, so that the original broad V-shaped cross-section of the xylem takes on a U-shape, and finally closes completely into an O-shape. The same result is often to be observed in the fusion of collateral bundles in the nodal anastomoses of the aerial stems. A fuller consideration of the origin and phylogenetic significance of the amphivasal bundles is reserved for a later page.

Very commonly in rhizomes of this type there is a dense plexus of transverse and oblique fibro-vascular strands in the surface of the central cylinder, just inside the endodermis. Fig. 10 represents a radial section through this region. This superficial plexus in many cases undoubtedly affords the chief mechanical support to the central cylinder, while to it are attached all of the root-strands and many of the smaller leaf-trace bundles. The larger leaf-trace bundles, on the other hand, like the ramular bundles, pass inward to the medulla and then outward to the superficial plexus, following a course very similar to that figured by De Bary for the Palm-stem (B, Fig. 1). It should be noted in passing that fully 90 per cent. of the branching and anastomosing of bundles in the rhizome takes place in the superficial plexus.

As an example of the Centrivasae we may examine more in detail the root-stock of *Scirpus americanus*, Pers. (*S. pungens*, Vahl), a form in which the internodes are long and the leaves reduced to the merest brown scales. Here the central cylinder (Fig. 16) is less compact; the bundles are much less numerous, and collateral throughout; the peridesm is only slightly developed, as is also true of the endodermal sheath; there is no dense

superficial plexus of fibro-vascular strands. The phloem-mass of each bundle is made up of a few rather large, very thin-walled sieve-tubes, with undoubted companion-cells lying in the angles between them. The xylem consists of usually two large vessels and a few small tracheids arranged in the conventional broad V-shaped section, at the point of which the protoxylem-lacuna is often conspicuously developed. At the nodes root-strands are attached directly to the superficial bundles of the cylinder, while the inconspicuous leaf-trace bundles pass inward to fuse with the medullary strands. The course of these bundles may be represented quite satisfactorily by Mohl's original diagram of the bundles of the Palm-stem (A, Fig. 1).

The fusion takes place by the strands becoming approximated laterally, phloem upon phloem, and xylem upon xylem. The union of the phloem elements is accomplished much more promptly than is that of the xylem-elements, as a result of which the xylem occasionally forms a semicircular zone about the inner side of the phloem. In no instance, however, has a true amphivasal bundle been found in the rhizome of this species, either at an ordinary node or at the origin of a branch.

Although the Amphivasae include a vast majority of the Cyperaceae, yet there are no great variations from the type in any essential feature of the structure of the central cylinder. The most striking irregularity appears in the development of the peridesm, which may be almost wholly undifferentiated in *Eleocharis*, uniformly two- or three-layered in *Scleria* and some Carices, or restricted to a few relatively enormous masses in certain species of *Eriophorum*. The endodermis is always well defined, and projected some distance upon outgoing strands, except at the origin of aerial shoots, where the cortex and medulla are in free communication. The bundles are always relatively numerous, and there is always more or less evidence of a superficial plexus, though this is less marked in *Eleocharis*.

The Centrivasae, though very few, present a range of variability quite as wide as the larger group. The medulla varies from cavernous in *Dulichium* and *Cladium* to densely sclerotic in *Scirpus robustus*; the peridesm may be centripetally massed in *S. rivularis* and *Dulichium*, or wholly undifferentiated in *S. microcarpus*; the endodermis may be reinforced to an unusual and unique degree as in *S. fluviatilis*, of a quite normal type as in *Dulichium* and *S. robustus*, or apparently quite wanting in *S. microcarpus*; finally, there may be a well-developed superficial fibro-vascular plexus, as in *S. fluviatilis*, or there may be nothing of the kind, as in *Cladium*. There is free communication between cortex and medulla through all foliar and ramular gaps in this group except in *S. fluviatilis*, in which the peculiar sclerotic jacket mentioned above closely encases the central cylinder of the rhizome in every part, even cutting directly across

the base of the aerial stem and closely investing the outgoing bundles for some distance. This jacket consists of about three layers of somewhat elongated, pointed or irregular, thick-walled, profusely pitted cells, of a more or less tracheidal appearance, with the longer axis radially disposed, and arranged in a dense zone bordering directly upon the outside of a little-differentiated endodermis. This peculiar sheath is apparently unique, and duplicated in no other species in the entire Order.

The accompanying Table I presents in concise form the more salient features of the rhizome in the more interesting species studied. Besides the species named in the table, some twenty other Carices have been examined, together with a few additional species of *Scirpus*, *Eleocharis*, and *Fimbristylis*. For purposes of confirmation and comparison, a study has been made of species of *Juncus*, *Streptopus*, *Pontederia*, various grasses, &c.

The more striking features of the rhizome of the Cyperaceae may be summarized briefly in the following key, based chiefly upon the generic characters of the central cylinder.

Generic Key to the Cyperaceae.

I. Centrivasae. Bundles of the rhizome collateral, or rarely amphivasal at the periphery.
  1. Medulla cavernous.
    a. Endodermis and peridesm conspicuously sclerotic . . *Dulichium*.
    b. Endodermis and peridesm not sclerified . . . . *Cladium*.
  2. Medulla not cavernous.
    a. Endodermis not apparent . . . . . *Scirpus microcarpus*.
    b. Endodermis distinct.
      aa. Simple, medulla thin-walled . . . . . *Scirpus americanus*.
      bb. With sclerotic medulla . . . . . *Scirpus robustus*.
      cc. With external sclerotic zone continuous across base of culm . . . . . *Scirpus fluviatilis*.

II. Amphivasae. Bundles of the rhizome all amphivasal.
  1. Peridesm only slightly developed, or undifferentiated.
    a. Medulla aerenchymatous . . . . . *Stenophyllus*.
    b. Medulla compact.
      aa. Rhizome tuberous . . . . . *Lipocarpha*.
      bb. Rhizome not tuberous.
        aaa. Small, bundles few . . . . . *Eleocharis*.
        bbb. Small, bundles many . . . . . *Scleria*.
        ccc. Large, bundles very many . . . . *Cyperus Papyrus*.
  2. Peridesm uniformly well developed.
    a. Rhizome tuberous . . . . . *Kyllinga*.
    b. Rhizome not tuberous.
      aa. Internodes long, xylem elements large . . . . . *Carex*.
      bb. Internodes short, xylem elements small, few . . *Hemicarpha*.

3. Peridesm more or less massed centripetally.
   a. Rhizome tuberous, or the internodes very short.
      aa. Endodermis not reinforced.
         aaa. Cortex very aerenchymatous . . . . . *Psilocarya.*
         bbb. Cortex compact or sclerotic . . . . . *Cyperus.*
      bb. Endodermis reinforced by sclerotic zone . . . *Fuirena.*
   b. Rhizome elongated, not tuberous.
      aa. Medulla sclerotic . . . . . *Rhynchospora.*
      bb. Medulla not sclerotic.
         aaa. Xylem elements few.
            aaaa. Peridesm slightly developed . . *Eriophorum* (in part).
            bbbb. Peridesm very strongly developed in four or five central bundles . . . *E. Scheuchzeri, E. alpinum.*
            cccc. Peridesm well developed in all of the central bundles . . . . . *Dichromena.*
         bbb. Xylem elements many.
            aaaa. Peridesm slightly developed . . . . *Fimbristylis.*
            bbbb. Peridesm very largely developed in all central bundles . . . . . *Scirpus* (chiefly).

TABLE I. Rhizome Characters. (Explanation.)

The symbols + and −, when standing alone or before another descriptive symbol, have a numerical significance, as 'many' or 'few.' When they follow another symbol they have a purely qualifying meaning, signifying that the preceding character is either well developed or the contrary. The qualifying symbol is doubled for emphasis.

1. Class: A, Amphivasae; or C, Centrivasae.
2. Form: t, tuberous; s, with short internodes; or l, with long internodes.
3. Central cylinder: c, compact or small; l, loose or large.
4. Endodermis: +, reinforced; −, simple; or 0, undifferentiated.
5. Medulla: a, aerenchymatous; c, compact; or s, sclerotic.
6. Bundles: s, scattered; or c, crowded.
7. Xylem elements: l, large; s, small; +, many; or −, few.
8. Peridesm: =, uniform; c, centripetal; or 0, undifferentiated.
9. Cortex: a, aerenchymatous; c, compact; or s, sclerotic.
10. Hypoderm: s, complete sheath; or r, ribs.
11. Tannin: +, much; −, little; or 0, absent.
12. Starch: +, much; −, little; or 0, absent.

The Aerial Stem.

The aerial stem or culm of the Cyperaceae presents a considerable variety of forms. In *Cyperus* and *Eleocharis* it assumes practically a scapose habit, with a few small or moderately large leaves clustered at its base, and terminated above by the simple or compound inflorescence,

which is naked in *Eleocharis*, and provided with large leafy bracts in *Cyperus*. The great majority of the Cyperaceae, however, possess a jointed culm with a few or many rather long internodes. The lower node commonly bears only a reduced or sometimes even scale-like leaf, while the larger leaves occur higher up the stem. The leaf-base always forms a closed sheath for some distance above its node of attachment.

The culm of *Dulichium* is cylindrical. The same is true of some species of *Eleocharis* in the young stages, but most of these are more or less flattened in the mature condition. *E. mutata* is unique in that its culm is sharply quadrangular with concave surfaces. With these few exceptions the culm of the Cyperaceae is triangular in cross-section; sometimes more or less obscurely so, owing to the convexity of the surfaces, as in *Scirpus lacustris*, *S. Californicus*, *S. caespitosus*, &c.; or with very sharp angles, as in *S. robustus*, *S. americanus*, some Carices, &c.

As previously stated, and as described by Pax (36), the aerial stem is commonly derived from the rhizome by a bifurcation of the growing point of the latter organ. In some cases numerous aerial stems arise from the root-stock by small lateral buds, as in *Eriophorum alpinum*. In still other cases the culm is terminal upon the short rhizome, as in short tuberous and annual species of *Cyperus*, *Psilocarya*, *Stenophyllus*, &c. At the point of origin of the aerial stem there is an extensive gap in the endodermal sheath of the rhizome, and through this gap the cortex and medulla are in free communication. The one unique exception to this rule is found in *Scirpus fluviatilis*, which has been described on a previous page. The bundles of the first leaf-sheath are derived from the superficial plexus of the central cylinder of the rhizome, while the cauline bundles are continuous with the deep-seated medullary strands. As these latter bundles begin to turn upward they branch more or less profusely, so that the number of bundles in the base of the culm is usually considerably greater than the number of rhizome strands to which they are directly traceable. Moreover, it is to be noted that these bundles of the culm-base are always collateral, whatever the nature of the rhizome strands from which they are derived.

The apical development of the culm has been studied by Miss Anderssohn (1), Guillaud (19), and Van Tieghem (56). It presents no features of special interest in the present investigation beyond the fact that here, as in some other Monocotyledons, cambial activity continues for some time after complete differentiation of the fibro-vascular bundles. We shall have occasion to refer to this fact again presently.

Dulichium is the only hollow-stemmed form among the Cyperaceae. *Eleocharis*, a few aquatic species of *Scirpus*, and *Cyperus Papyrus* possess very large medullary air-spaces, separated by delicate plates of parenchyma; and many other species present this feature in a much less conspicuous

TABLE I.

Rhizome.	Class.	Form.	Central Cylinder.	Endoderm.	Medulla.	Bundles.	Xylem Elements.	Peridesm.	Cortex.	Hypoderm.	Tannin.	Starch.
Cyperus flavescens, L.	A –	t	l	–	c	–	– s	0 –	c	r –	+	–
,, *rivularis*, Kunth	A –	t	l	– –	c –	– –	– l	0c	c –	r –	–	– –
,, *Nuttallii*, Eddy	A –	t	l	– 0	c	– s	– s	c –	c	r	+	–
,, *dentatus*, Torr.	A –	t	l	–	c	–	– l	0c –	a –	r –	–	–
,, *strigosus*, L.	A –	t	l	0 –	c	+	+ s	0	c	r –	+ +	–
,, *filiculmis*, Vahl	A	st	c	–	s –	–	+	= 0	s –	r –	+	+
,, *Grayi*, Torr.	A –	st	c –	– +	c +	–	–	= c	s –	r –	–	– –
,, *alternifolius*, L.	A	s	c –	– +	c –	c	– l	0c	c –	r +	+	+
,, *Papyrus*, L.	A –	s	l	+	c	+ +	– l	0 –	c	r	+	+
Kyllinga pumila, Michx.	A –	st –	l	–	c –	+	– l	=	c	r –	–	– –
Dulichium arundinaceum (L.), Brit.	C –	l	c –	–	c	c –	– l	c +	c	0	+	–
Eleocharis mutata (L.), R. and S.	A	s	l –	–	c	sl	–	= 0	a +	r – –	–	0
,, *ovata*, R. and S.	A	st –	l	–	c	– s	– l	0	a	r –	–	0
,, *palustris*, R. and S.	A +	s –	l	+	s –	– s	– l	0	a +	r +	+	0
,, *acicularis*, R. and S.	A –	s	c	–	c	– –	– s	0	c	r –	– –	0
,, *tuberculosa*, R. and S.	A	s	l	–	c –	+	– s	0c –	c –	r	+	–
,, *rostellata*, Torr.	A	s	l	+	c	– s	– l	0	c	r +	–	–
Dichromena latifolia, Baldw.	A	l –	l	+	c –	s –	–	c +	c	r – –	+	–
Psilocarya scirpoides, Torr.	A –	st	l	–	c	+ l	– s	c –	a –	r	–	0
Stenophyllus capillaris, Britton	A – –	st	c	+ –	a –	– l	– s	0	c –	0	– –	– –
Fimbristylis castanea (Michx.), Vahl	A –	st –	c	–	c	c +	+	c +	c	sr +	+	–
,, *laxa*, Vahl	A	s	c	+ –	c	c	+	= c –	c	0	+	– –
,, *autumnalis* (L.), R. and S.	A	s	c –	–	c –	c –	+ –	= 0	c	0	– –	0
,, *Warei*	A –	st	c –	–	c	+	–	c –	c –	0	–	0

| | | |

degree. A form of aerenchyma is found in the medulla of several species of *Scirpus*, notably *S. fluviatilis*, *S. atrovirens*, and *S. microcarpus*, and in *Fuirena* and *Stenophyllus*. Elsewhere the medulla is usually more or less compact. Sclerosis is conspicuously developed in the nodal diaphragms of *Dulichium* and in the nodal regions of *Scirpus robustus*, *Fuirena*, and certain species of *Eriophorum* and *Carex*.

The sclerotic tissue of the cortical region presents a number of types of adaptation to mechanical purposes, as described by Schwendener (47). In some cases there is a dense hypodermal zone of sclerenchyma, while in other forms the mechanical tissue may be confined to numerous or few, large or small hypodermal ribs, or these may even give place entirely to a zone of assimilatory tissue which is not infrequently in the form of typical palisade cells. Following in part the suggestion of Rickli (40), we may divide the Cyperaceae into two classes, based upon the relative prominence of mechanical and assimilatory tissue in the cortex. Those forms which possess but little mechanical sclerenchyma in the cortex, but which show well-developed assimilatory tissue and numerous stomata, may be termed the Chlorocyperaceae. To this group naturally belong those species which are scapose in habit, or of which the leaves are much reduced in size or number. On the other hand, those forms in which the assimilatory mechanism gives place wholly or in large measure to sclerenchymatous elements may properly be called the Sclerocyperaceae.

As typical of the first class we may consider the culm of *Scirpus robustus*, a cross-section of which is shown in Fig. 11. It will be observed that the fibro-vascular bundles are collateral, not numerous, and scattered irregularly throughout the section. The medulla contains very large schizogenous air-spaces separated by plates of parenchyma only one cell thick. The medullary bundles lie at the intersections of these plates. It should be noted in passing that these large air-chambers are divided into compartments by occasional transverse partitions or 'bulkheads.' De Bary (12) has shown that these partitions are made up of dense tissue in species growing in dry situations, while in aquatic species the partitions are composed of thin-walled, stellate cells similar to those found in the medullary plates of certain Juncaceae. Frequently the fibro-vascular bundles anastomose in their course, in which case the transverse strands lie in these 'bulkheads.'

The epidermis is covered by a thin cuticle, which in some small amphibious species is distinctly papillate. Numerous somewhat depressed stomata open into the thick assimilatory zone, which is made up of two or three layers of typical palisade cells. The mechanical tissue of the stem is reduced to a few very small hypodermal ribs and a few sclerenchyma strands embedded in the inner margin of the palisade

zone. The figure of *Eleocharis* (Fig. 12) represents another type of this class, in which the medullary tissue is still further reduced, and the assimilatory zone is quite undifferentiated.

We may now examine the culm of *Scirpus cyperinus* as a fair type of the Sclerocyperaceae, though it is by no means an extreme example of the sclerotic habit. As shown in Fig. 5, the bundles of the internode are fairly numerous, collateral, and with centripetally massed peridesm. The bundles of the outermost series alternate with rather large irregular air-spaces. It should be observed in passing that these air-spaces differ from those occurring in the medulla of the Chlorocyperaceae in that they are lysigenous, or rhexigenous, according to De Bary (12). The medulla consists of thin-walled parenchyma, which in this species shows a tendency to break down in mature stems. The epidermis is covered by a thin, smooth cuticle. In species which show conspicuous hypodermal ribs, as in *S. robustus*, the epidermal cells are very much smaller over these ribs than elsewhere. In *S. cyperinus* the epidermis shows no stomata, and is subtended by a continuous zone of sclerenchyma which in very many cases is produced into strong ribs which connect internally with the peridesm of the interlacunar bundles. The more general anatomical features of the aerial stems of the Cyperaceae studied in the present investigation are briefly set forth in Table II.

TABLE II. AERIAL STEM CHARACTERS. (EXPLANATION.)

The symbols + and − are used here with the same variations in significance as already indicated in Table I.

1. Class: S, Sclerocyperaceae; or C, Chlorocyperaceae.
2. Form: t, triangular; q, quadrangular; r, round; s, scapose; or j, jointed.
3. Medulla: a, aerenchymatous; c, compact; s, sclerotic; or 0, a large lacuna.
4. Cortical Air-spaces: +, numerous; −, few; or 0, none.
5. Cauline Bundles: s, scattered, few; or c, crowded, many.
6. Peridesm: =, uniform; c, centripetal; 0, undifferentiated; or ×, joined in a continuous mechanical zone.
7. Cortical Bundles: +, many; −, few; or 0, none.
8. Hypodermal Sheath: +, strongly developed; −, slightly developed; or 0, wanting.
9. Hypodermal Ribs: +, numerous; −, small or few; or 0, none.
10. Palisade and Stomata: +, well developed; −, poorly developed; or 0, absent.
11. Tannin-sacs: +, many; −, few; or 0, none.
12. Bundles of Leaf-trace: average number, where observed.

TABLE II.

Aerial Stem.	Class.	Form.	Medulla.	Cortical Air-spaces.	Cauline Bundles.	Pericæsum.	Cortical Bundles.	Hypodermal Sheath.	Hypodermal Ribs.	Palisade and Stomata.	Tannin Sacs.	Bundles of Leaf-sheath.
Cyperus flavescens, L.	C—	sr—	c	+	—	=—	—?	0	—	—	—	?
,, *rivularis*, Kunth	C—	st—	c—	—	——	=c	0	0	——	—	——	?
,, *Nuttallii*, Eddy	C—	st—	c	+	—	—c—	+?	0	+	—	—	30?
,, *denudatus*, Torr.	C	sr	c	+	—	0	0	0	——	—	—	?
,, *strigosus*, L.	C—	st	a—	o	c—	=c	0	0	+	—	—	25
,, *filiculmis*, Vahl	C—	st	c+	o	—	=	0	0	+	—	—	?
,, *Grayi*, Torr	C—	st	c	o	—	=c	0	0	+	—	—	?
,, *alternifolius*, L.	C—	st	c	o	s	=c—	0	0	+	—	—	?
,, *Papyrus*, L.	C	st—	a+	o	s+	0	?	0	+	o	—	?
Kyllinga pumila, Michx.	C—	ji—	c	—	—s	=	—	0	—	—	—	?
Dulichium arundinaceum (L.), R. and S.	C—	jr	0	+	—	c+	+	0	—	—	+	50
Eleocharis mutata (L.), R. and S.	C+	sq+	a+ +	o	—s	—c	0	0	+	+	+	?
,, *ovata*, R. and S.	C+	sr	a+ +	o	—s	=	0	0	+	+	+	?
,, *palustris*, R. and S.	C	sh—	a+ +	o	—— s	—c—	0	0	+	—	—	?
,, *acicularis*, R. and S.	C	sr—	a+ +	o	—	=	0	0	—	+	—	?
,, *tuberculosa*, R. and S.	C+	sr—	a+ +	o	——	=	0	0	+	—	—	?
,, *rostellata*, Torr.	C	sr	a+ +	o	—	=—	0	0	+ —	+	—	?
Dichromena latifolia, Baldw.	C—	jr—	c	—	—	c—	—	0	—	+	—	?
Psilocarya scirpoides, Torr.	S—	ji—	a—	+ +	—c	xc—	0	0	0	o	—	30
Stenophyllus capillaris, Britton	C—	jr—	a+	—	——	=—	0	0	—	—	—	?
Fimbristylis castanea (Michx.), Vahl	C—	ji—	a	o	—s	—c—	0	0	—	—	—	?
,, *laxa*, Vahl	C	jr—	a+	—	——	=c	—	0	—	—	—	?
,, *autumnalis* (L.), R. and S.	C—	jr—	a—	—	—	=	——	0	+	—	—	?
,, *Warei*	S—	jr—	c	—	—	=	——	0	+ +	—	—	25

| | | |

At this point it is proper to call attention to the fact that evidence of cambial activity has been observed in the internodal bundles of practically all the examples of the Cyperaceae which have been studied. Fig. 6 is taken from a section near the base of an internode of *S. cyperinus.* The cambial nature of the zone between xylem and phloem in this instance can scarcely be questioned, as it comes well within the definition of 'cambium,' as originally laid down by De Bary (12). We certainly do not have here a 'closed' collateral bundle such as is commonly represented as being the exclusive type among the Monocotyledons. Queva (38) has demonstrated a similar cambium in *Gloriosa,* Guillaud (19) observed a persistent cambiform tissue in *Canna,* and Miss Sargant (43) cites still other examples. Through the kindness of Dr. Chrysler, the writer has been able to examine sections of several grasses, some of which show a far more typically developed cambium than has hitherto been described in the Monocotyledons. It should be said, however, that it happens in certain instances that the xylem and phloem are completely separated in the mature bundle by a plate of sclerotic tissue, as shown in Fig. 13 of *Dulichium,* and as described by De Bary (12) for species of *Rhapis* and *Calamus.* More or less complete lignification of the phloem, such as that observed in *Helianthus* by Boodle (3), occurs in *Fuirena* and species of *Eriophorum.*

We have now to consider the structure of the nodes, and the course of the bundles through the stem. A study of the nodal structures represented in Figs. 7, 8, 9 from *Scirpus cyperinus* will make it evident that the arrangement of the fibro-vascular elements of the stem is profoundly disturbed at this point. Moreover, other parts of the structure are often specially modified in this region. The medulla is usually more compact, if not, indeed, sclerotic; and it is of less breadth, owing to the encroachment of the anastomosing fibro-vascular strands. There are no cortical air-spaces, and in the jointed Chlorocyperaceae the assimilatory zone is either much reduced at the nodes or is even entirely wanting. The longitudinal extent of the nodal plexus varies from less than half a millimetre in *Dulichium* and the slender Carices to over half a centimetre in *Scirpus sylvaticus* and large plants of *Carex comosa.*

Approaching the node from below, the first indication of a departure from the simple internodal condition is seen in the interlacunar bundles of the cortex. Here the xylem-elements rapidly increase in number, spreading around the phloem in a broad U-shaped mass. The arms of the U next become involuted in such a manner as to include a portion of phloem on either side of the original phloem, after which the small lateral amphivasal strands separate off from the main central narrow V-shaped strand thus: oVo. This stage is represented, though in a somewhat complicated form, in Fig. 7. Passing to a slightly higher

level, the small lateral amphivasal strands are seen to pass divergently obliquely inward and upward, where they anastomose with similar strands from adjacent cortical bundles, forming a dense circular plexus of amphivasal strands, to which are added strands from the peripheral zone of proper cauline bundles, which here bend more or less sharply inward to pass into the base of the next internode. A little higher up (Fig. 8) we find the general anastomosis extending to the remainder of the bundles, practically all of which assume the amphivasal character for at least a short distance at some part of their course through the nodal complex. The latest evidence of nodal irregularity, as we pass upward into the internode, is to be seen in the deeper-seated medullary bundles. The central strand from the original cortical bundle passes upward and sometimes slightly outward into the leaf-sheath. In other words, it is a bundle of the leaf-trace. From the circular plexus already described are developed new peripheral strands which pass upward as the cortical bundles of the next internode.

It appears that there is a remarkable constancy in the number of cortical bundles in the several internodes of a given plant, and, indeed, of a species. However, the number of cauline bundles usually decreases considerably from the base upward. Thus, in an average specimen of *S. cyperinus*, the cortical bundles numbered about forty in each internode; the cauline bundles in the first internode were eighty-seven, in the second eighty-two, in the third seventy-six, in the fourth seventy, in the fifth sixty-six, and in the sixth (just below the inflorescence) sixty-eight. In the first branch of the inflorescence there were twenty bundles, and in its subtending bract thirty, while in the main axis above this branch there were thirty-five bundles.

In *Dulichium* we find the fibro-vascular system of the Cyperaceae occurring in its simplest form, and a study of the course of the bundles in this group may lead to a clearer conception of the state of things in the highly complicated *Scirpus cyperinus*. Here the bundles of the internode are arranged in two circles only. The outer bundles alternate with the large air-spaces, and are clearly cortical bundles. The inner circle constitutes the cauline system. At the nodes there is formed a circular plexus uniting all of these bundles by amphivasal strands. These strands are given off from the bundles almost at right angles, and consequently there is little or no evidence of amphivasal bundles in the transverse section. A section through the upper part of the node shows three series of bundles—the outer series continuous below with the cortical series, but now passing off into the leaf-sheath; the inner series continuous below with the cauline series, and itself the cauline series of the next higher internode; the middle series, newly derived from the circular plexus, and constituting the cortical series

of the next higher internode. The diagrams of Fig. 2 and the photographic Figs. 13, 14, will serve to make this point quite clear. And in the light of these facts the diagram G, Fig. 1, will convey a more or less correct idea of the course of the bundles in the stem of *Scirpus cyperinus*, which is in this respect typical of the greater part of the Cyperaceae.

It appears evident, then, that the bundles of the leaf-trace in most Cyperaceae do not enter the cauline system of the stem at the point of insertion of the leaf, either in the manner described by Mohl (33), De Bary (12), and Kny (32), for the Palms, or in that found by Falkenberg (16), Queva (39), and Chrysler (9), among the Liliales. The arrangement more nearly resembles that observed by Guillaud (19) in the cortical bundles of the rhizome of *Acorus calamus* (D, Fig. 1), with this important difference—that in the Cyperaceae *all* of the bundles of the leaf-trace pass down through one internode as cortical bundles. Consequently we find in the bundle arrangement of the aerial stem of most Cyperaceae nothing in common with Mohl's Palm type ; and the 'reparatory bundles' described by Queva (38), as occurring in *Gloriosa*, and observed by the writer in a confirmatory study of *Streptopus*, are here to be found, if at all, in the peripheral cauline bundles rather than in the medullary ones.

Cortical bundles are of quite general occurrence in many widely separated groups of plants. Wossidlo (62) has described a dense anastomosing cortical system in the *Cocos* type of Palm. Wittmack (59) showed that the cortical strands in *Musa ensete* are connected by re-entrant anastomoses at the nodes with the cauline system, and De Bary (12) describes a similar re-entrant connexion of the amphivasal bundles in the secondary thickening of *Dracaena*. Sanio (41) considered the so-called sieve-tube strands in the cortex of *Elodea* to be greatly reduced cortical fibro-vascular bundles. More recently Hartog (22) has found typical cortical bundles in the Lecythideae (Myrtales) and in the Barringtoneae, while Boodle and Worsdell (5) have found less typical cortical strands in *Casuarina*. Col (10) describes cortical bundles in several Dicotyledonous plants, and gives an admirable summary of the literature upon the subject of bundle-distribution.

De Bary (12) indicates four general modes of arrangement of cortical bundles, as follows :—Firstly, all bundles of the leaf-trace enter the cauline system at the same node, after passing as cortical bundles through one or more internodes below the insertion of the leaf. Here De Bary places *Casuarina* and *Osmunda*, with single leaf-trace bundles ; species of *Begonia*, *Aspidium*, *Pteris*, *Cyathea*, &c., with several leaf-trace bundles ; and Rhipsalidaceae, with peculiar winged stems. Evidently we may now add to these the majority of the Cyperaceae with jointed culms. Secondly, the central leaf-trace bundle enters the central cylinder directly, while the lateral bundles pass down through the cortex to the next node.

Here are certain Calycanthaceae and Melastomaceae, in the first of which the cortical bundles show a reversed orientation of xylem and phloem. Thirdly, the central and larger lateral leaf-bundles enter directly, while the marginal bundles become cortical, as in certain Aroideae, Palmae, Bromeliaceae, and most of the Scitamineae. Fourthly, it rarely happens that the middle leaf-trace bundle passes down through the cortex to a lower node, while the lateral strands join directly with the cauline system, as in *Arceuthobium*.

Van Tieghem (56) has suggested a possible explanation of the cortical course of the leaf-trace upon the hypothesis that the leaf-sheath has fused with the stem for one or more internodes above its actual origin. Some weight is lent to this view by the mode of leaf-insertion observed by the writer in *Streptopus*. Here, especially in *S. amplexifolius*, the margins of the leaf-base are frequently fused with the stem for two centimetres or more above the nodal complex.

In the scapose Cyperaceae the bundles of the involucral bracts enter the stem in a broad curve and unite with the medullary bundles at the basal part of the nodal complex, in a manner very like that prevailing among the Liliales. A similar mode of leaf-insertion is found in the nodes of *Scirpus robustus*. Accordingly, these forms show no cortical fibro-vascular bundles, though the deep-seated cortical sclerenchyma strands may be vestigial indications of a cortical system of bundles.

The culm of the Cyperaceae does not normally branch except in giving rise to the axes of the inflorescence. However, abortive axillary buds are of very common occurrence. The fibro-vascular strands supplying these buds are always collateral, and may be traced downward to their insertion upon the cauline bundles just below the nodal plexus. They have no direct connexion with the leaf-trace, differing in this respect from the axillary buds of certain Liliales described by Queva (38), and also from those of *Alchemilla* described by De Candolle (13), as well as from the Palm type of Mohl (33). It is important to note that in the Cyperaceae the ramular bundles have nothing to do with the nodal amphivasal plexus, contrary to the principles laid down by Queva (38), in connexion with his study of *Gloriosa*. This point will be referred to again in considering the floral axis.

The Leaf.

The narrow linear leaves of the Cyperaceae, without exception, present a strongly xerophytic type of structure. In all cases they surround the stem for a considerable distance by a closed sheathing base. The free lamina is usually deeply grooved, presenting a V-shaped cross-section in the narrower forms, while the broader ones show a horizontal portion extending outward from the end of each arm of the V, as in *Carex lupulina*.

The amount of mechanical tissue is relatively very large, and the mesophyll is sometimes almost wholly lacking in the mature condition, owing to the development of large air-cavities in the body of the leaf. The parallel fibro-vascular bundles or 'veins' are very numerous, there being as many as sixty in some species. The middle one is considerably larger than the average, and in the broader leaves the bundle at the top of each arm of the V is also larger, so that in this case there are three principal veins. The bundles are always collateral, with well-developed peridesm, which is produced from each pole into a strong hypodermal rib. The assimilatory zone is rarely differentiated into a true palisade layer. The upper epidermis is covered by a strong cuticle, and is frequently developed into short, sharp, sclerotic spines, especially along the margins of the leaf. Over the hypodermal ribs the epidermal cells are smaller and thinner-walled, as already seen in the stem, and as described by De Bary (12) and Spinner (50). The epidermis of the under surface is thinner-walled, and commonly bears more or less conspicuous cuticular 'pegs' or papillae, at least in all aquatic and limicolous species. The stomata are relatively few and usually somewhat depressed. In their essential structural features the leaves of the Cyperaceae show little, if any, more variation than do the roots. Eichler (15) and Trécul (52) have shown that the leaf of the Cyperaceae is basipetal in its growth, and that the fibro-vascular strands are projected inward to their insertion upon the cauline system.

Both Guillaud (19) and Gwynne-Vaughan (20) have emphasized the great importance of the leaf in the Monocotyledons as a determining factor in the development of the central cylinder of the stem. The latter observer points out the fact that in the apical growth of the young stem the terminal cone is altogether insignificant in comparison with the latest-formed leaf, and the procambial strands of the young leaf are more numerous and larger than those of the cauline ring where first differentiated.

We have already alluded to the fact, established by the investigations of Chrysler (9) and others, that in an early stage of its growth the stem of a monocotyledonous plant has its fibro-vascular elements disposed in a single circle of collateral strands, and that it is only at a later stage that medullary strands, collateral or amphivasal, make their appearance. That is to say, it is only after the introduction of a number of leaf-traces into the cauline system that we find the characteristic Monocotyledonous type and arrangement of bundles making their appearance. It is a well-known fact that the leaf-trace of the Monocotyledons is made up of a far greater number of bundles than is that of any other group, and, as Jeffrey (30) points out, it is probably the accommodation of this large number of incurrent bundles that accounts for the dense nodal complexes which are so common a feature of this group. These bundles do not end blindly in the medulla, according to the ancient doctrine of Desfontaines, but each

of them, from its very nature, must find attachment on the cauline system in order to be of any service in the economy of the plant. Accordingly the leaf-trace strands invest the cauline strands with a network of vascular elements, giving them an amphivasal character, which may be lost again in the internode by reorientation, or subdivision, as in the culms of the Glumales, or which may persist throughout, as in the rhizomes of the Cyperaceae and in the subterranean stems of many Arales and Liliales. The whole matter may be summed up in the statement that among the Monocotyledons the leaf is the dominant organ in determining the characteristic stelar development.

The Floral Axis.

The inflorescence of the Cyperaceae, with a few exceptions such as *Dulichium* and some Carices, is terminal upon the culm. It occurs in the form of a head, a spike, or a single or compound umbel. Caruel's (7) observations upon the structure and development of the floral organs indicate that there is in this subject a wide and interesting field for investigation. However, this matter is worthy of separate and special treatment, and we shall not attempt to consider it here.

The particular fact to which we would direct present attention is the reduction in number and characteristic arrangement of the bundles in the floral axis. This axis arises from the terminal node of the culm, except in the cases mentioned above, where it is axillary. In case the leaves of the involucre are large, this node shows amphivasal bundles, which may even be continuous through the short internodes of the involucroid region, as in *Cyperus strigosus*; but if the involucral scales are small or absent the bundles in the node are not amphivasal, as in *Eleocharis*. The bundles of the axis are seen to be continuous with the cauline system below the node. Passing upward in the axis these bundles quickly arrange themselves in a single circle, from which strands are given off to the individual florets. Each floral trace arises from two adjacent strands of the cylinder, leaving the gap between them considerably wider as it passes off. On the way obliquely outward through the cortex the trace separates into two parts—an outer, slender strand, which is the trace of the subtending scale or glume; and an inner, larger, double mass, which later breaks up into a circle of extremely delicate strands which pass to the floral organs proper. Fig. 20 will serve to make these facts quite clear, so far as the structure of the central cylinder is concerned. It is to be observed that the bundles are here arranged in a single circle, and that there is no indication whatever of the amphivasal condition. There is a very remarkable uniformity in this respect throughout the entire Order. The structure prevailing in this region cannot fail to remind one of the arrangement already described as occurring in the young seedling of the Monocotyledons, and, in turn, of that present

in the mature axis of the Dicotyledons. If we bear in mind the fact that in the floral axis of the Cyperaceae there are no large and numerous incurrent leaf-trace bundles, we should not be surprised to find here retained the primitive siphonostelic central cylinder. And, conversely, if we find that this primitive arrangement of the stelar elements is disturbed only where there are large and numerous incurrent leaf-trace bundles, we are certainly justified in the statement previously made regarding the dominance of the Monocotyledonous leaf in determining characteristic stelar development. The significance of these facts will be considered more at length presently.

Fossil Cyperaceae.

According to Seward (49) there were probably no Monocotyledons earlier than the Cretaceous period. Owing to the soft structure of primitive plants of this group, their preservation is rendered most unlikely. At any rate, it has been shown conclusively by the investigations of Scott (48) and others that the supposed Monocotyledons of remotest antiquity were in reality primitive Gymnosperms. Certainly no Cyperaceae have been described as from earlier than the Tertiary period. Heer (24) mentions a somewhat doubtful *Cyperacites Dallensis* from the early part of that epoch. By the close of the Tertiary the grasses and sedges were fully established. Schimper (44) describes for that period eleven Carices, eight species of *Cyperus*, thirty-three *Cyperacites*, and a number of more or less doubtful Cyperaceous forms. Hartz (23) has recently described typical spikes of *Dulichium* as occurring in the interglacial beds of Southern Jutland, Denmark.

Phylogenetic Considerations.

The primitive ancestral Cyperaceous type is necessarily more or less a matter of conjecture. Among the earliest known fossils of this Order we find the two widely divergent genera *Carex* and *Cyperus*, occurring in about the middle of the Tertiary epoch. Apparently we must look to a considerably more remote period for the common ancestor of these forms. That is to say, the primitive Cyperaceous stock probably extended back well into the beginnings of the Monocotyledons as a whole, and consequently we should expect to find in this Order some indication of the original characters of the division. Miss Sargant (43) has expressed a tentative view that the ancestral Monocotyledons were geophilous in habit. However, this habit usually implies a more or less xerophytic type of structure; certainly, at least, a well-developed mechanical system in some part of the plant. But we have seen that the geological record of the Cyperaceae is blank prior to the appearance of species of *Carex* and *Cyperus*, which would indicate that their ancestors must have been of a less enduring type of structure.

In view of these facts, we are inclined to adopt the hypothesis sug-

gested by Jeffrey (30) and others, to the effect that the Monocotyledonous prototype was aquatic in habit, of soft, loose texture, and provided with large leaves. Moreover, these primitive Monocotyledons were in all probability fresh-water forms, for otherwise they must have taken on a xerophytic structure, as a result of which they no doubt would have been preserved somewhere in the geological record. Indeed, we may venture the opinion that this is precisely what did happen in the course of time to the primitive Cyperaceae. Driven by torrential currents or the drying-up of streams, these ancestral sedges became adapted to the dry banks, or were carried into humus bogs and salt marshes. By the first course we might very readily derive the tuberous *Cyperus*; by the second, the long rhizome of *Carex*. By either course we should expect the plant rapidly to lose its hydrophytic character, with reduction of fundamental tissue and consequent decrease in size of members. At the same time, the more conservative fibro-vascular system would respond much less quickly to this reduction process, and the stelar structure would grow more and more compact, with all the attendant phenomena of nodal complexes, amphivasal bundles, medullary strands, and cortical leaf-traces.

Apparently such an extreme degree of specialization and comparative isolation as that shown by the genus *Carex* could have been reached only through a very long period of adaptation. Hence we may consider *Carex* to be a highly-developed, relatively modern genus, derived from a successful early variant from the primitive Cyperaceous stock. *Cyperus*, with few exceptions, presents the tuberous, scapose habit and a high degree of uniformity in structural details. While *Carex* and *Cyperus* are thus seen to be very clearly defined and somewhat divergent genera, each presenting a fairly striking degree of structural unity, it appears that *Scirpus* presents the opposite extreme of great variability. It alone of the entire Order refuses to fit as a whole into any scheme of morphological or anatomical classification. In *Scirpus* we find both Chlorocyperaceae and Sclerocyperaceae; both Amphivasae and Centrivasae; both scapose and jointed culms. Altogether the genus appears to be anatomically in the 'experimental stage'; the focus of evolutionary activity in the Order; the terminal bud, so to speak, of this particular phylogenetic branch. These facts, however, do not necessarily indicate that the genus is a recently established one, but that it may be a somewhat ancient and generalized type.

As for the more intimate phylogenetic relations of the various genera of the Cyperaceae, it must be conceded that the whole matter is at best highly problematic, and we shall venture to add only the most general statements in regard to it. On anatomical grounds it seems reasonable to place *Kyllinga*, *Dichromena*, *Fuirena*, *Hemicarpha*, and *Lipocarpha* on the side of *Cyperus*, though probably of more recent derivation; *Rhynchospora*, *Cladium*, and *Scleria* tend strongly toward *Carex*; while *Psilocarya*,

Stenophyllus, *Fimbristylis*, and *Eriophorum* seem to lie more directly in the line of descent of *Scirpus*. *Eleocharis* is apparently a long-established and much reduced limicolous genus from near the common origin of the Order. *Dulichium* is probably a highly specialized but less successful early variant from the central line of descent.

From what has already been said it will appear that the Cyperaceae are a relatively primitive group among the Monocotyledons, and that they have suffered a considerable morphological reduction and specialization in acquiring their present amphibious to xerophytic mode of life. Their closest affinities appear to be with the Juncaceae on the one hand, and with the Gramineae on the other. Upon embryological evidence Van Tieghem (56) concludes that the Cyperaceae serve as the connecting link between the true Monocotyledons and the so-called anisocotyledonous Gramineae. This view, however, is not supported by the facts observed by Miss Sargant (43) in her extensive studies of the cotyledon of the Monocotyledons. At all events, anatomical evidence points to a somewhat intimate relationship between the two groups. Nevertheless, they are clearly marked off from each other by morphological differences in the structure of the culm, the arrangement and insertion of leaves, the character of floral parts, and in the pronounced difference in character and occurrence of amphivasal bundles.

In the work on cotyledonary development already cited, Miss Sargant (43) ably supports the view that the Monocotyledons are derived from the Dicotyledons, or that both spring from a common Angiospermous ancestry. The evidence afforded by the developmental and morphological data accumulated by recent investigators renders the correctness of this view highly probable. We may now add to this evidence the facts learned from our study of the Cyperaceae. (1) It is to be recalled that in the young condition of the seedling of this group the central cylinder is typically tubular as in the Dicotyledons. (2) The same tubular type of central cylinder is of universal occurrence in the floral axis of the Cyperaceae. (3) It is only where large and numerous leaf-trace bundles enter the central cylinder that we find the typical Monocotyledonous type and arrangement of stelar elements. Hence we may conclude that the type of central cylinder found in the conservative seedling and floral axis is ancestral or palingenetic, while the medullary and amphivasal bundles occurring elsewhere are more recently acquired or caenogenetic features. But those stelar characters which we find to be palingenetic in the Monocotyledonous axis are precisely those which are observed to be characteristic of the stelar system of the Dicotyledons. In so far, then, as the anatomical characters of the Cyperaceae are of importance, they point somewhat strongly to a common ancestry of the two grand divisions of Angiospermous plants.

Summary and Conclusions.

In the course of the present investigation a somewhat careful study has been made of the structural characters of some eighty species of Cyperaceae, representing seventeen North American genera. In addition to these, representatives of several other Monocotyledonous groups have been examined by way of confirmation and comparison. The following conclusions, based upon the results of this study, may be offered in answer to the questions propounded in the introductory paragraphs:—

1. Amphivasal fibro-vascular bundles are continuous throughout all Cyperaceous rhizomes which bear conspicuous leaves at all of the nodes, and in which the internodes are relatively short (Amphivasae). Such bundles are absent from the rhizome only where the leaves are very small and widely scattered (Centrivasae).

2. In the culms of the Cyperaceae amphivasal fibro-vascular bundles commonly occur only in the nodal complexes; rarely such bundles are continuous through the very short internodes of the involucroid region of certain species. Elsewhere the bundles of the culm are strictly collateral.

3. Amphivasal bundles are derived from collateral bundles by the multiplication of xylem-elements, resulting from the introduction of large and numerous leaf-traces into the central cylinder. In the Cyperaceae the amphivasal condition is not in any way related to the phenomenon of branching.

4. A study of the Cyperaceae shows that the leaf is the dominant factor in the development of the stelar characteristics of the Monocotyledons. Branching of the axis does not affect the nature of the fibro-vascular bundles.

5. The foliar fibro-vascular bundles pass downward through the culm as cortical bundles to the next lower node, where they fuse with the cauline bundles and with the subtending leaf-trace, through a ring-like amphivasal plexus. The cauline bundles pass continuously, but with nodal anastomoses, from the base of the culm to their termination in axillary buds or floral axes, or, less frequently, in nodal complexes. In the rhizome the course of the bundles more nearly resembles that which is typical of the Palm-stem. Fusions and anastomoses of the bundles of the rhizome take place chiefly in the superficial reticulum of the central cylinder.

6. The simple tubular central cylinder which has been found in the seedling and the floral axis proper of all the Cyperaceae which have been examined is to be considered ancestral or palingenetic; while medullary strands and the amphivasal bundles characteristic of most rhizomes and of the nodal complexes of aerial stems apparently must be regarded as more recently acquired or caenogenetic features.

7. On anatomical grounds the Cyperaceae appear to be one of the more primitive groups among the Monocotyledons, considerably specialized and reduced from the common megaphyllous, possibly hygrophilous ancestor. They present a high degree of anatomical unity, not only in floral and foliar characters, but also in their internal structure, and especially in the mode of occurrence, number, and development of their amphivasal bundles.

8. The anatomy of the Cyperaceae seems to point strongly to the derivation of the Monocotyledons and Dicotyledons from a common ancestry which presented characters essentially Dicotyledonous in the arrangement and structure of fibro-vascular bundles, and in the presence of cambial growth.

In conclusion, I desire to express my obligations to Professor L. L. Hudson, of Delaware, Ohio; to Professor S. F. Poole, of Wichita, Kan.; to Miss Helen Plowman, of Greenville, Ohio; and to Mr. A. H. Moore, Mr. J. G. Hall, and Mr. M. L. Fernald, of Cambridge, Mass., for material; and, above all, to Professor E. C. Jeffrey, for material and for the many suggestions and criticisms offered throughout the course of this investigation.

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EXPLANATION OF THE FIGURES

Illustrating Mr. Plowman's paper on Cyperaceae.

Fig. 1. Diagrams illustrating the course of the fibro-vascular bundles in various Monocotyledonous stems. The broken lines represent the imaginary inner boundaries of the cortical zone, while the nodes are indicated by the horizontal lines. *A*, Mohl's plan of the Palm type. *B*, De Bary's plan of the distichous Palm type. *C*, plan of bundles in the rhizome of *Convallaria majalis*. *D*, plan of bundles in the rhizome of *Acorus Calamus*. *E*, plan of bundles in the stem of *Tradescantia virginica*. *F*, plan of bundles in the rhizome of *Luzula campestris*. *G*, plan of bundles in the aerial stem of *Scirpus cyperinus*. (*C*, *D*, *E*, and *F* adapted from Guillaud.)

Fig. 2. Diagrammatic representation of the course of the fibro-vascular bundles in the aerial stem of *Dulichium arundinaceum*. *A*, transverse section of part of stem just above a node, including the leaf-sheath. *B*, section passing through the nodal complex. *C*, section some distance below the node. *D*, projection of fibro-vascular elements from tangential section. *E*, radial longitudinal section of the stem. *a.c.l.*, air-cavity in leaf; *a.c.s.*, cortical air-space; *c.b.*, cortical bundles; *l.b.*, leaf-bundle; *l.t.*, leaf-trace bundle; *n.a.*, nodal anastomosis; *n.d.*, nodal diaphragm; *n.p.*, nodal plexus; *s.b.*, cauline bundle; *l.*, leaf.

PLATE I.

Fig. 3. Part of a transverse section of the rhizome of *Scirpus cyperinus*, showing typical amphivasal bundles in the central cylinder, and centripetal massing of the peridesm in part of the bundles. A type of the Amphivasae. × 50.

Fig. 4. High-power detail of the same, showing endodermal cells thickened on the inner wall, and peripheral amphivasal bundles with but slightly differentiated peridesm. × 175.

Fig. 5. Part of a cross-section of an internode in the culm of *Scirpus cyperinus*, showing cortical and cauline fibro-vascular bundles, cortical air-spaces, and hypodermal sclerotic zone. A type of the Sclerocyperaceae. × 40.

Fig. 6. Collateral fibro-vascular bundle from a transverse section near the base of an internode of the culm of *Scirpus cyperinus*, showing the type of cambial development commonly occurring in this region of Cyperaceous culms. × 350.

Fig. 7. Part of a transverse section of the culm of *Scirpus cyperinus*, taken just at the base of the nodal region, showing the beginning of division in the cortical bundles to form the annular anastomosis. × 75.

Fig. 8. Part of a transverse section through the middle of a node of an aerial stem of *Scirpus cyperinus*. Most of the fibro-vascular bundles show the amphivasal condition; a few are collateral, while certain ones show intermediate conditions. × 50.

Fig. 9. Part of a radial longitudinal section through a node of the culm of *Scirpus cyperinus*, showing the annular amphivasal bundles of the nodal complex in cross-section. The base of the leaf-sheath appears above at the right. × 40.

Fig. 10. Part of a radial longitudinal section of a rhizome of *Scirpus cyperinus*. The endodermis is just to the right of the centre. On the right is the cortex, showing a leaf-trace on the extreme margin. To the left is the outer portion of the central cylinder, with the circular amphivasal strands of the superficial reticulum appearing in cross-section. × 40.

Fig. 11. Part of a transverse section through an internode of the culm of *Scirpus robustus*. A type of the Chlorocyperaceae, with large medullary air-spaces, well-developed palisade layer, and numerous stomata. × 75.

Fig. 12. Part of a transverse section through the culm of *Eleocharis palustris*, showing extreme reduction of the tissues. A few stellate 'bulkhead' cells are shown on the left. × 75.

Fig. 13. Part of a transverse section of the culm of *Dulichium arundinaceum*, just above a node, showing a section of the leaf-sheath externally, and the two circles of bundles in the stem, the inner of which is the proper cauline series, and the outer or cortical series, alternating with large air-spaces. × 30.

Fig. 14. Part of a slightly oblique transverse section through a node of the culm of *Dulichium*. The portion at the right is the lower, showing two series of bundles. At the left the section passes into the upper part of the node, where there are three series of bundles: the inner, or cauline; the outer, or leaf-trace; and the middle, or cortical series of the next higher internode. The central part of the figure shows the nodal anastomosis, with part of the nodal diaphragm below. × 20.

PLATE II.

Fig. 15. Part of a transverse section of the rhizome of *Scirpus fluviatilis*, showing the peculiar sclerotic zone outside the endodermis. × 50.

Fig. 16. Part of a transverse section of the rhizome of *Scirpus americanus*. A type of the Centrivasae. × 60.

Fig. 17. Transverse section of the central cylinder of the rhizome of *Carex lupulina*. A type of the Amphivasae. × 20.

Fig. 18. Part of a transverse section of the central cylinder of the rhizome of *Cladium mariscoides*. Cavernous medulla and cortex, and endodermis hardly distinguishable. × 50.

Fig. 19. Part of a transverse section of the rhizome of *Eleocharis palustris*. × 40.

Fig. 20. Transverse section of the axis of the inflorescence of *Eleocharis palustris*, showing the simple tubular central cylinder which is characteristic of the floral axis proper throughout the Cyperaceae. × 25.

Note.—The nomenclature embodied in this paper is based chiefly upon that found in Gray's Manual, sixth edition, and in the Flora of Britton and Brown, edition of 1896. Upon more critical study, and after a comparison with the results of recent investigations in this field, it appears that the following corrections are desirable:—

For *Scirpus microcarpus*, Presl, read *Scirpus rubrotinctus*, Fernald.

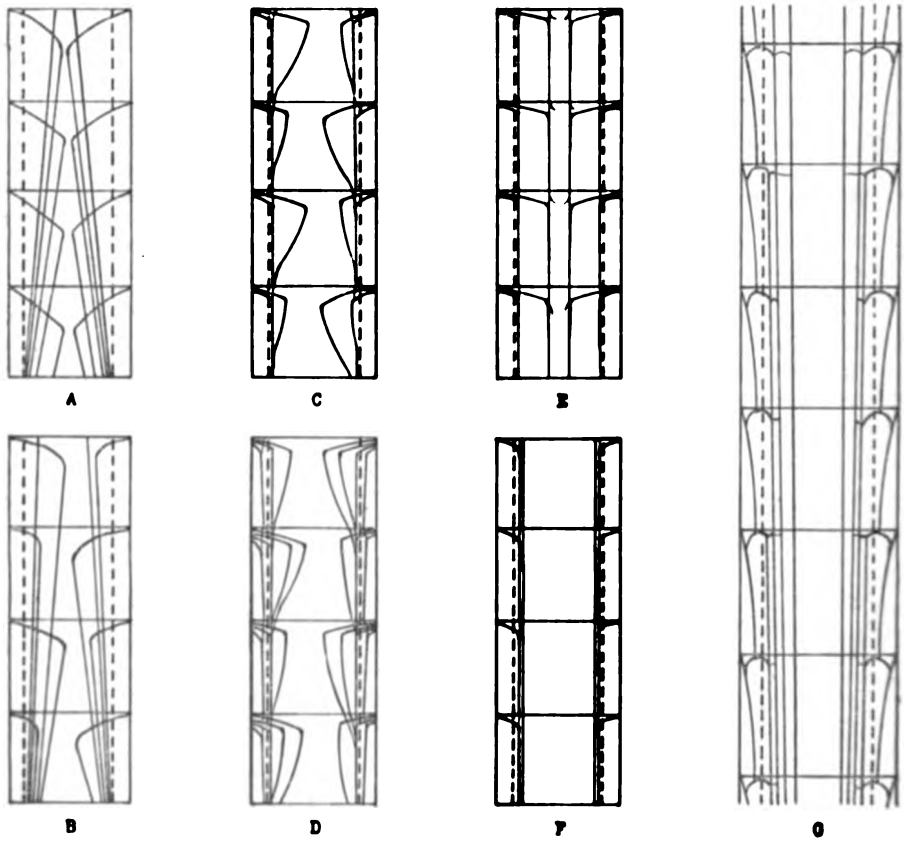
For *Eleocharis ovata*, R. & S., read *Eleocharis obtusa*, Schultes.

For *Eriophorum gracile*, Koch, read *Eriophorum tenellum*, Nutt.

For *Eriophorum vaginatum*, L., read *Eriophorum callitrix*, Cham.

On these matters see Rhodora, ii, 1900, p. 20, and vii, 1905, pp. 85–87. Also Proc. Am. Acad. Sci., xxxiv, 1899, p. 492.

The writer is indebted to Mr. M. L. Fernald, of the Gray Herbarium, for these facts.



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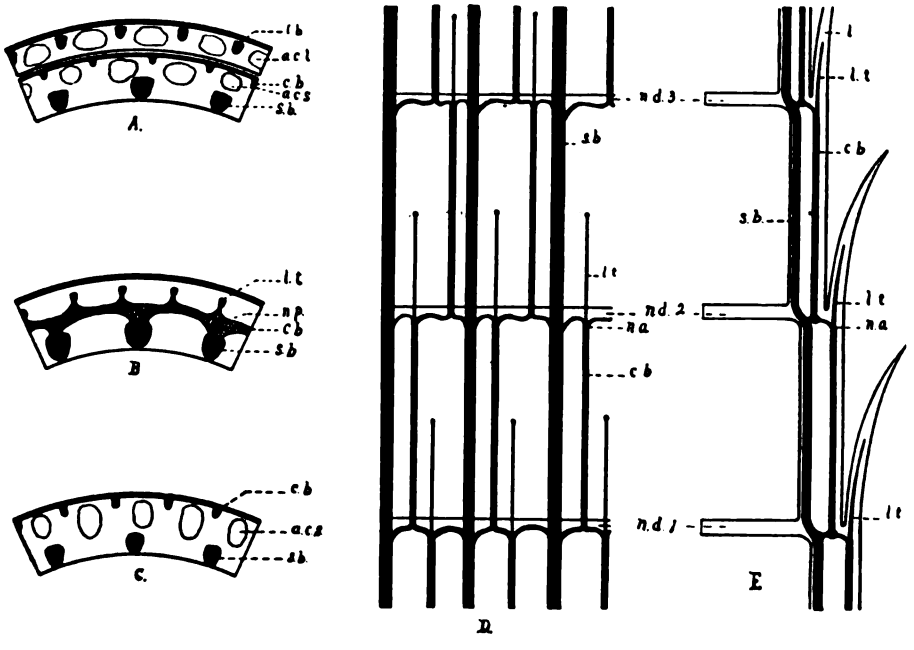
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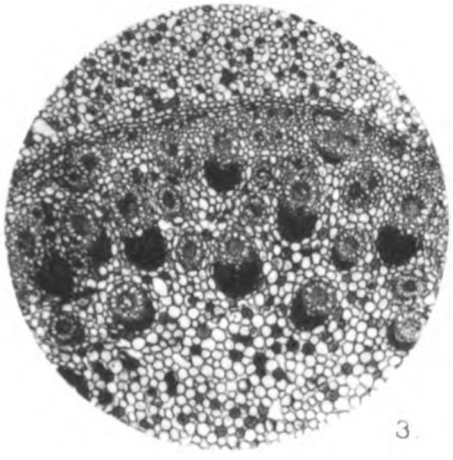
FIG. 2.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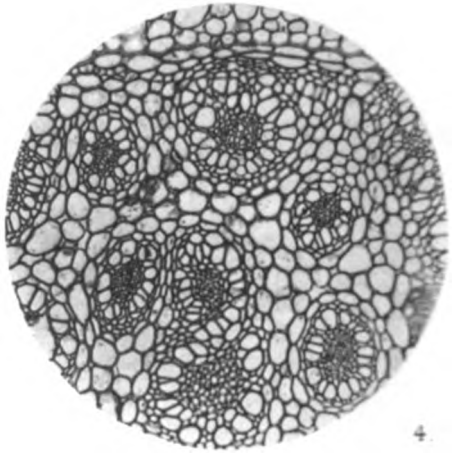
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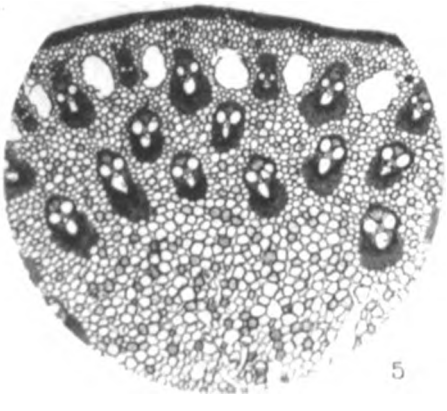
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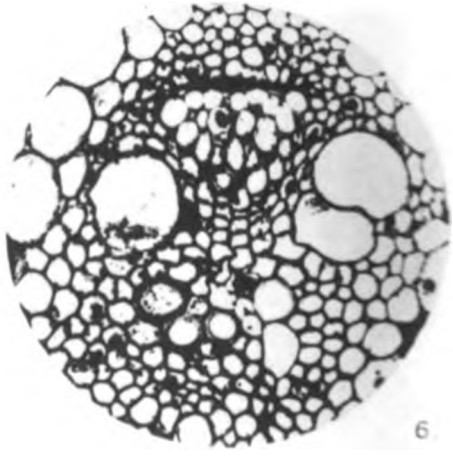
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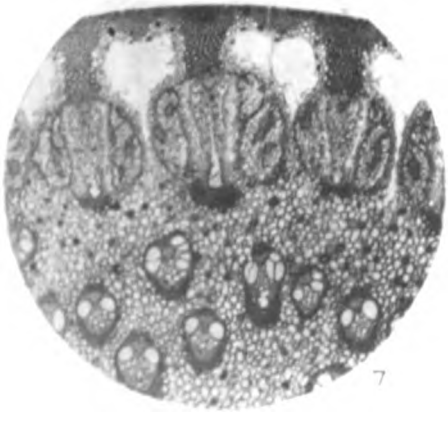
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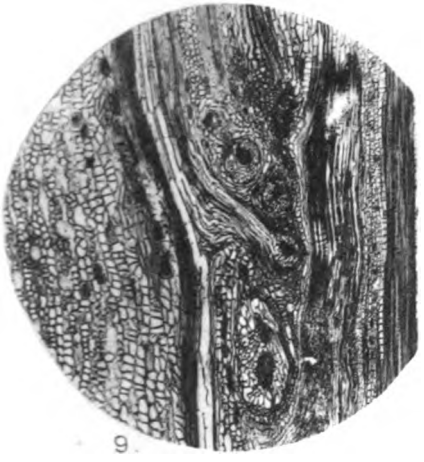

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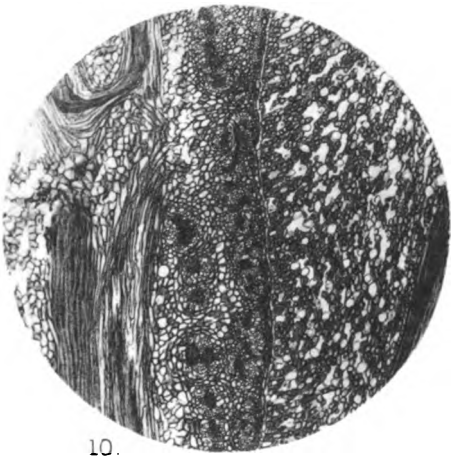

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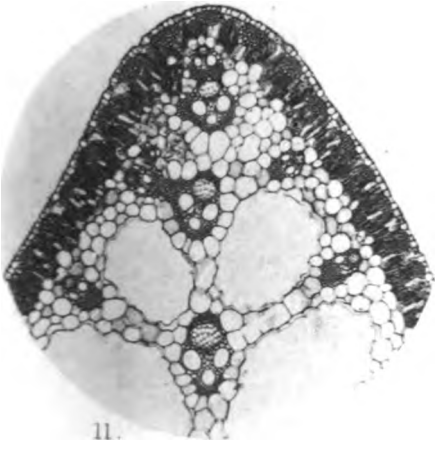

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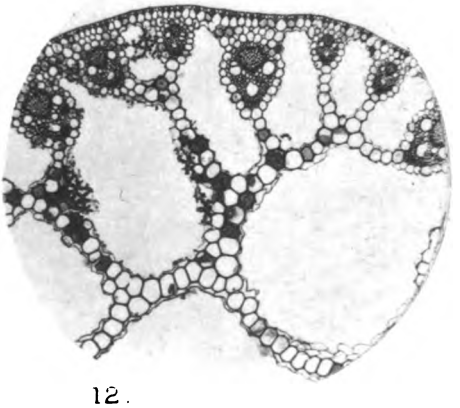

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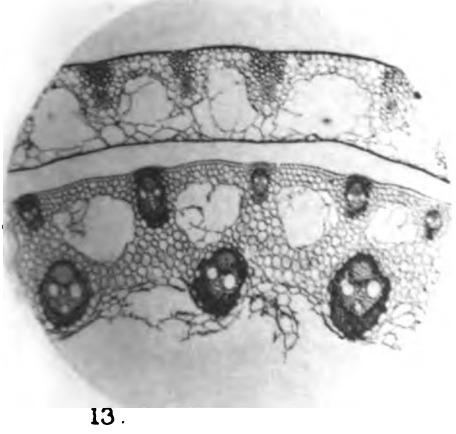

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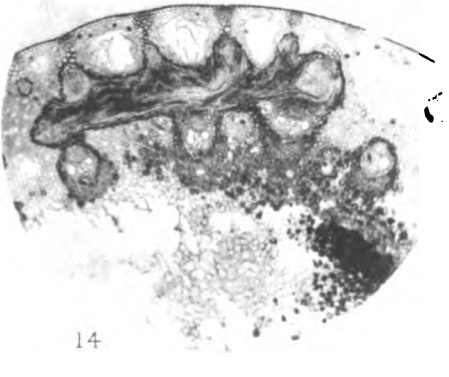

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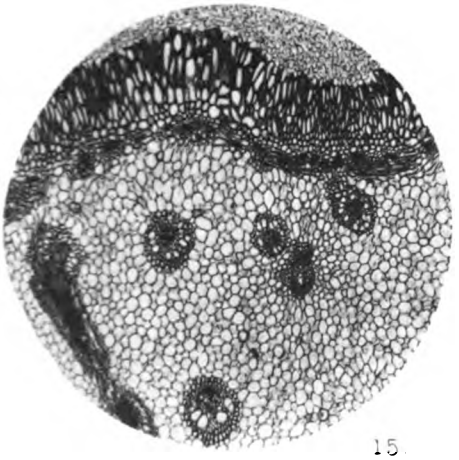

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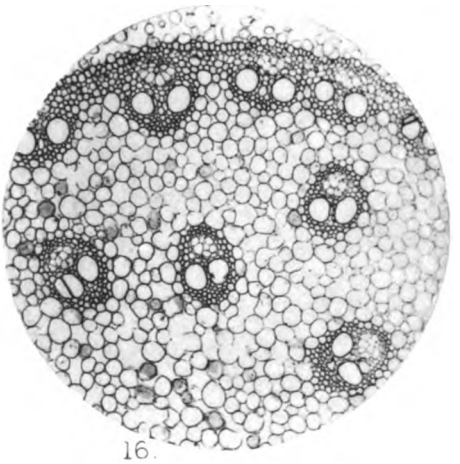

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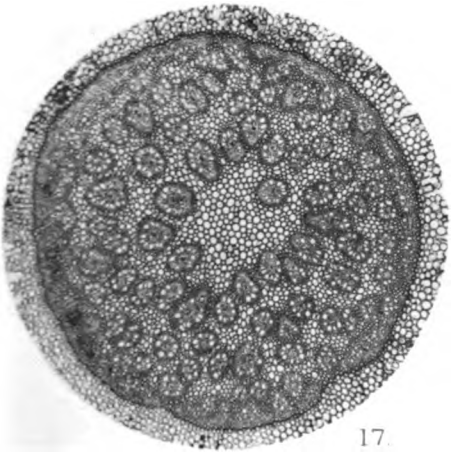

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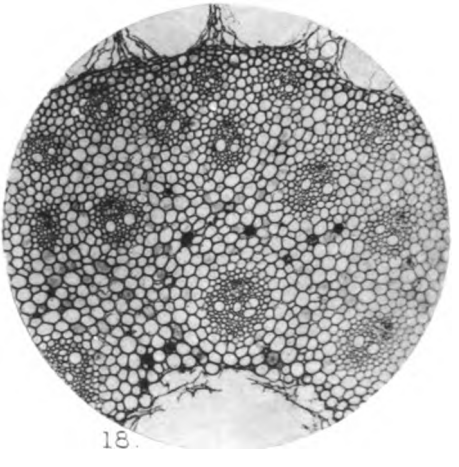

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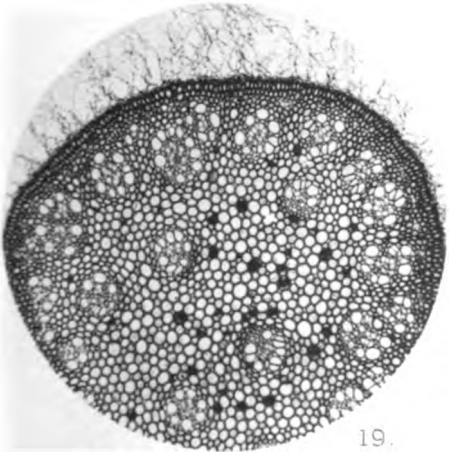

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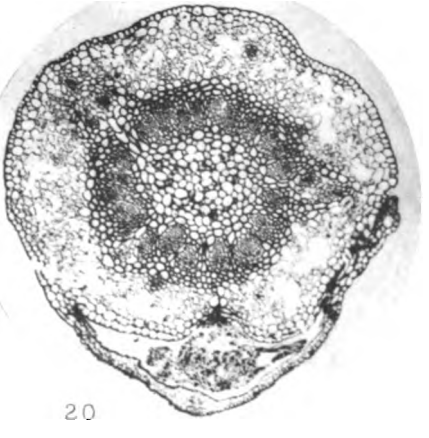

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A.B.P. photo. Huth, London.

PLOWMAN—ANATOMY OF CYPERACEAE.

Further Studies on the Sexuality of the Uredineae.

BY

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AND

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With Plates III and IV.

EARLIER studies by one of us (1) have shown that in the aecidium of *Phragmidium violaceum* a peculiar process occurs, in which the nucleus of an ordinary vegetative cell migrates into a special 'fertile cell,' which then develops actively and gives origin to a series of binucleate aecidiospores and intercalary cells, the two nuclei always dividing by a process of conjugate division. This fertile cell was considered to be a female cell, and its union with the vegetative cell a 'reduced sexual process' in which the latter cell replaces the now functionless male cell (spermatium).

These further studies were undertaken to ascertain how far this process would explain *generally* the origin of the conjugate nuclear condition which is known to be constant in the cells of the aecidium which produce the aecidiospore-rows. The development of the typical aecidium with its definite pseudoperidium, and its comparatively deep point of origin in the tissues of the host, obviously required cytological investigation for comparison with that of *Phragmidium*. For in that genus the aecidium (the so-called caeoma) is of very simple type, consisting merely of a single layer of fertile cells developed directly beneath the epidermis, and bounded only by a few paraphyses; and even these may sometimes be absent.

It was also hoped that further investigation might throw some light on the cytological life-history of the reduced forms which, possessing no aecidium, yet show cells with conjugate nuclei at some stage of development, the paired nuclei fusing sooner or later in the teleutospore.

While this work was in progress a very interesting paper appeared

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by Christman (3), in which he showed that in certain forms (*Phragmidium speciosum*, *Caeoma nitens*, and *Uromyces Caladii*) the sexual process was very different from that observed in *P. violaccum*. In the aecidia of these forms fusion in pairs takes place between the uninucleate fertile cells; cells with conjugate nuclei are thus produced, which then undergo a series of rapid divisions and produce the aecidiospores in the usual way.

We have been able to confirm the existence of this type of fusion in the aecidium of one form which we investigated, and there is no doubt that it must be given equal rank with nuclear migration as a method of aecidium development; but we are not able to accept Christman's interpretation of his results. He looks upon the process he observed as a mere conjugation of undifferentiated gametes; and though he comments on two such different types of sexual development occurring in the same genus, *Phragmidium*, he makes no attempt to bring them into line.

If, however, the view be accepted that the fertile cells of *P. violaceum* represent female gametes, which are now fertilized by vegetative cells instead of by male cells (the now functionless spermatia), it follows that the cells which fuse in *P. speciosum*—since the structure and development of the aecidium is exactly the same in the two cases—also represent *female cells, which now conjugate in pairs*. By such a very simple interpretation the two processes are reduced to a common term. The two species of *Phragmidium* are then seen to exhibit merely two different methods of dealing with the same problem—fertilization in the absence of the male cell. In the one case the male cell is replaced by a vegetative cell, in the other by another female cell.

If, on the other hand, Christman's view of the behaviour of *P. speciosum* be accepted, it must also apply to *P. violaceum*, and it leads to the unsatisfactory conclusion that the fertile cells here also represent undifferentiated gametes, which for some obscure reason have given up fusing in pairs, and now fuse with vegetative cells instead.

The view put forward above obviously explains the relation of the two processes throughout the group, and has the further advantage of giving a reasonable explanation of the structure and occurrence of the spermatia, which in Christman's view are left out of account.

That the conjugation of female gametes may take place in the absence of the appropriate male cells is shown clearly by the authors' studies on *Humaria granulata* (2), where, in the absence of the antheridium, the female nuclei of the ascogonium fuse in pairs.

The forms investigated were *Uromyces Poae*, Raben., *Puccinia Poarum*, Niels, and *Melampsora Rostrupi*, Wagn., for the development of the aecidia, and *Puccinia Malvacearum*, Mont., *Puccinia Adoxae*, DC., *Uromyces Ficariae*, Lév., and *Uromyces Scillarum*, Wint.

The material was fixed in Flemming's weaker fluid or in acetic alcohol (20 or 25 per cent. sol. of the acid in absolute alcohol). The latter fluid does not fix so well as that of Flemming, but is much more penetrating, and was always used when an air-pump was not available; without the use of such an instrument watery fluids will not satisfactorily fix the portions of leaves. Benda's iron-haematoxylin followed by a one per cent. watery solution of Congo-red, as already described (2), was found the most satisfactory stain.

In addition to the cytological observations mentioned in the earlier paper (1), the general morphology of the aecidium has been investigated by De Bary, Neumann (6), and Richards (7).

Uromyces Poae, Raben.

This is a heteroecious *eu-* form with its spermogonial and aecidial stage on *Ranunculus Ficaria*. Material was obtained in April and fixed in acetic alcohol.

The vegetative mycelium of the Fungus is found ramifying among the cells of the leaf and petiole, and occasionally of the young fruit. The hyphae exhibit single nuclei, usually in separate cells, as was observed earlier by Sapin-Trouffy (8).

The spermogonia appear early on the upper side of the leaf and have the typical flask-shaped structure, being very similar to those of *Puccinia graminis*. The spermatia (Pl. III, Fig. 10) have the large nucleus and the reduced cytoplasm which has been pointed out in the earlier paper (1) as characteristic of these cells throughout the group. They take no part in aecidium development and are, as usual, without apparent function.

The first indication of the young aecidium is a mass of tangled hyphae, which develops directly below the epidermis on the under side of the leaf; in the petiole this mass may be placed a little deeper. The group of hyphae increases in size and soon shows a differentiation into two sharply marked portions, a lower consisting of a mass of closely packed hyphae composed of short, uninucleate cells with dense contents, and an upper consisting of large irregular hyphae which are almost completely empty (Fig. 1). The large empty cells seem to be derived, at least in part, from the lower small-celled hyphae with dense contents, for cells cut off from the latter can be seen enlarging and losing their contents.

The nuclei of the cells with granular contents contain in the resting state a very well marked nucleolus, but the chromatin is very small in amount, and both it and the nuclear membrane stain with great difficulty. This nuclear structure is characteristic of all the cells of the aecidium, so that in ordinary lightly stained preparations the nucleus appears as a deeply staining large granule, the nucleolus, surrounded by a light

area (Pl. III, Figs. 1–4). It is only in exceptional cases or in material in which the cytoplasm has been much overstained that a nuclear reticulum can be clearly made out (Fig. 8).

As development of the young aecidium proceeds the cells with dense contents become somewhat larger, and their origin from hyphal rows of cells less obvious. The next stage is that among the mass of dense uninucleate cells a few binucleate ones appear, and these have increased somewhat in size (Fig. 2). More and more cells gradually become binucleate and arrange themselves into a definite layer. These binucleate cells are the 'fertile cells' of the aecidium, and it is from them that the rows of aecidiospores and intercalary cells are derived, the fertile cells forming the basal layer of the aecidium (Fig. 7).

Before they become binucleate the fertile cells are not very clearly defined, but at the stage of development, at which some of the cells with dense contents are changing from the uninucleate condition to that with paired nuclei, there can be observed migrations of nuclei from one cell into a cell which is still uninucleate. These nuclear migrations are much more difficult to observe than in the case of *Phragmidium violaceum*, for the 'fertile cells' are neither well defined when young, nor can progressive stages of development be observed in passing from the periphery to the centre of the aecidium. Thus migrations have to be sought for generally in the mass of mixed uninucleate and binucleate cells such as is found in the stage shown in Fig. 2.

Only a small number of migrations were clearly observed, but there can be little doubt that, as in *Phragmidium violaceum* (where numerous cases were observed), the condition of conjugate nuclei in the aecidium is normally brought about in this form by a process of nuclear migration into the special fertile cells.

The migrations were of the same type as those observed earlier in *Phragmidium*, the nucleus becoming very much constricted in its passage through the wall. In the present form, however, the nucleolus, being the only deeply staining portion of the nucleus, is the part that can be traced most easily through the wall. During the process it becomes stretched out into a band-like structure (Figs. 3–6) (often with a characteristic beaked appearance) in the formation of which the chromatin, no doubt, plays a small part.

No signs were observed of the fusion of the fertile cells in pairs as described by Christman, although on the appearance of that author's paper the preparations were carefully re-examined with that object in view.

Owing to the difficulty of distinguishing the fertile cells in the very young state the presence of definite sterile cells, as in *Phragmidium*, could not be made out with any certainty, although indications of them were observed in a few cases.

As development of the aecidium proceeds the fertile cells, aecidiospore-mother-cells, and spores become arranged in perfectly regular rows, and the hyphae below the aecidium become gradually emptied of their contents, which pass up into the fertile cells (Fig. 7). The intercalary cells are small and disappear early; the division which separates them from the aecidiospores being usually found in the second or third row of cells above the layer of fertile cells.

The development of the pseudoperidium from the outermost layer of 'fertile cells' is well shown in Fig. 7. These pseudoperidial cells exhibit very thick, finely striated walls, and their contents, with the two nuclei, soon become disorganized. In the young state, before it is ruptured, the pseudoperidium stretches like a protecting dome over the more or less hemispherical mass of developing fertile cells and aecidiospores (Fig. 7). The cells of the pseudoperidium appear to represent in this form aborted aecidiospore-mother-cells rather than aecidiospores, for no clear cases of the formation of intercalary cells were observed in them.

Some evidence was obtained in support of Richards' (7) observation that the terminal spores cut off from the central fertile cells (basidia of older authors) form the central part of the pseudoperidium, the peripheral part only being formed by the outermost layer of fertile cells; this point, however, was not investigated in detail.

Various stages of conjugate division (Figs. 9 *a–d*) were observed in the divisions which cut off the intercalary cells. The small simple spindles and the chromatin masses, without, apparently, any differentiation into chromosomes, were to be seen as described in the earlier paper (1); but in this case the minute size of the chromatin mass as compared with the large nucleolus is very striking.

As in the case of *Phragmidium violaceum*, fertile cells, and the spores derived from them, were sometimes observed which contained three nuclei, and in very rare cases four nuclei were to be seen. The trinucleate cells were not uncommon, and it was not unusual to observe three or four rows of such cells in one aecidium. Whether these abnormal numbers are due to the division of one or both of the conjugate nuclei, or to a process of multiple fertilization, it is at present impossible to say. It is to be noted that cells with more than two nuclei were observed by Richards (7) in some of the aecidia which he investigated, but Sapin-Trouffy makes no mention of them. The fate of the aecidiospores with more than two conjugate nuclei is also unknown; they might conceivably give rise to a mycelium with, for example, trinucleate cells and bearing trinucleate uredospores and teleutospores, but such has not been met with. It is possible, on the other hand, that they are incapable of germination.

PUCCINIA POARUM, Niels.

The spermogonial and aecidial stages of this heteroecious form are found on the leaves of *Tussilago Farfara*, the aecidia appearing as round whitish swellings in their very young state. *P. Poarum* is peculiar in having two crops of aecidiae in each year, one in the spring and one in the autumn; also two crops of uredospores and teleutospores arising from the aecidiospores. The material here investigated was obtained in early September.

The aecidia arise somewhat deeper in the leaf tissue than in the case of *Uromyces Poae*, but their general development is very similar. The fertile cells arise in the same way, though their early stages are even more irregular, and there is the same doubt as to the presence, or absence, of definite sterile cells.

Nuclear migrations (Figs. 12 and 13) of the usual type were observed in connexion with the differentiated fertile cells. It was noticed, however, that paired nuclei were also to be observed at a stage before the differentiation of the fertile layer, or in cells below that layer after its differentiation. This suggested that nuclear migrations might sometimes take place in cells which had not yet differentiated into fertile cells. This view proved to be justified; for besides the ordinary nuclear migrations mentioned above, one case was observed of a nuclear migration from one vegetative cell to another (Fig. 14). The cell so fertilized was just below the layer of fertile cells, and presumably it would either grow up directly into a fertile cell, or it might divide further before giving origin to the definite fertile cells.

We thus have in *P. Poarum* two types of nuclear migration in connexion with the development of the aecidium: one an ordinary nuclear migration (reduced fertilization) into a fertile (female) cell, the other a less common process, in which a vegetative cell is fertilized in a similar way, and later gives origin to a fertile cell or cells. The latter process is of great interest, for when it occurs the homologue of the female cell is actually fertilized from its very origin. It is as if the prothallial vegetative cells investigated by Farmer, Moore, and Digby (5) should, after fusing, produce an *oospore* (containing naturally the double number of chromosomes) from which the embryo arose later.

This form also was carefully examined for the fusion described in other cases by Christman (4), but no evidence of such a process could be obtained.

The development of the spores and of the pseudoperidium is the same as that of *Uromyces Poae*.

Cells with three and with four nuclei were observed in this form also, and a spore-mother-cell of each kind was seen in division (Figs. 15 and 16), showing clearly that in these abnormal cases there is true conjugate division.

Neither in this case nor in that of *Uromyces Poae* was any evidence obtained for the origin of the fertile cells from one or several special hyphae, as described for a number of forms by Richards (7). The latter author laid considerable stress on this point at the time, as tending to confirm a relationship between the aecidium and the ascocarp; but the work of recent years, which has so clearly established the fertile cells as independent sexual elements, reduces the exact origin of these cells to a point of little significance. The aecidium we now know is in no sense a definite morphological entity and cannot be compared with the ascocarp.

MELAMPSORA ROSTRUPI, Wagn.

The aecidial stage of this form occurs on *Mercurialis perennis*, and before its relation to the *Melampsora* on *Populus* was worked out by Rostrup it was known as *Caeoma Mercurialis*. The aecidium is of particular interest, for, like that of the Melampsoras generally, it is without a pseudoperidium, and, therefore, of the same type as that of *Phragmidium*.

A definite row of uninucleate fertile cells with sterile cells above is developed close beneath the epidermis just as in *Phragmidium*. Sometimes, however, it is, apparently, not a superficial cell of the mycelium which develops into the fertile and sterile cells, but a slightly lower cell; so that, later, one or two layers of small crushed cells are found above the sterile cells. The fertile cells become binucleate and then develop and produce rows of aecidiospores and intercalary cells in the typical way.

No evidence of nuclear migration could be observed in these cases, but the greater width of the binucleate cells giving origin to the aecidiospore rows as compared with that of the uninucleate fertile cells was noticeable; as was also the fact that two sterile cells could sometimes be clearly distinguished above the young binucleate cells (Fig. 17). This indicated that the conjugate nuclear condition was brought about by the fusion of cells as described by Christman. Owing to the age of the material the earliest stages of fusion were not observed, but very clear evidence of this fusion was obtained from later stages. In these cases the remains of the partition wall in the lower part of the cell were to be seen exactly as described by Christman (Figs. 17 and 18).

In *Melampsora Rostrupi*, then, we have the other type of reduced fertilization in which the fertile (female) cells fuse in pairs.

The cells of the aecidium produced in this way can no longer be termed 'fertile cells,' since they are the product of two such cells. A single term is, however, obviously convenient for the cells, whatever their origin, which give rise to the rows of aecidiospore and intercalary cells. As the

term basidia of the older workers is no longer applicable, they may simply be termed the *basal cells* of the aecidium, since they are the cells at the base of the special cell-rows.

Puccinia Malvacearum, Mont.

As is well known this parasite is one of the *lepto*-forms, i. e. there is only one kind of spore, the teleutospore, and this germinates in the sorus immediately on reaching maturity. The whole life-cycle is thus completed in a very short time, the teleutospore sorus beginning to appear about twelve days after infection.

As stated by Sapin-Trouffy the vegetative mycelium contains single nuclei. The first indication of the formation of a teleutospore sorus is the development of a tangled mass of uninucleate-celled hyphae, which is often more regular towards its edge (Fig. 19). Then directly on this mass hyphae with *conjugate nuclei* arise, and these usually produce an irregular mass of binucleate hyphae, on which arise the special cells that are later to give origin directly to the teleutospores (Fig. 20). These special cells produce one or more teleutospores (Figs. 21 and 22), and are very similar, though smaller in size, to the special cells described in an earlier paper for *Gymnosporangium clavariaeforme*.

Very careful search failed to reveal the exact method by which the transition from the single to the conjugate nuclear condition is brought about. The smallness of the cells and nuclei, and the absence of any regular row or group of cells—such as are found in the aecidia—on which attention can be concentrated in the hunt for nuclear migrations or cell-fusions, render the task of elucidating such a point almost hopeless. That the change of nuclear condition takes place at several different points in connexion with each sorus, and not once for all, is indicated by the general distribution of the binucleate hyphae which first appear.

Whether the conjugate condition of the nuclei is the result of either of the processes observed in the aecidium, or whether there is a still simpler process in which two sister nuclei themselves become conjugate in a cell, must remain unsettled. It must be remembered, however, that nuclear migration between vegetative cells has been seen to occur in *P. Poarum*. It is also interesting to note that, just as in the aecidium, we find, in connexion with teleutospore-formation, a certain number of abnormal cells and spores which show three nuclei (Figs. 22 and 23). The similarity of abnormality may perhaps be taken as indicating a similarity in the methods by which the conjugate nuclear condition is brought about in the aecidium and young teleutospore sorus respectively.

PUCCINIA ADOXAE, DC. AND UROMYCES SCILLARUM, Wint.

In these two *micro*-forms, in which the life-history is similarly reduced to its simplest state, young teleutospore sori were examined in early spring. In both these cases it was found that the general vegetative mycelium showed conjugate nuclei (Figs. 24 and 25).

In these cases, then, the change to the conjugate condition (i. e. the process of reduced fertilization) must take place very early, and the point at which it occurs can only be discovered by the careful investigation of material from the stage of infection by the sporidium.

The commonness of the binucleate condition of the sporidium at the time of infection might suggest that, in the two cases in question, the conjugate condition starts in the sporidium itself. This, of course, is possible, but it does not seem probable; for on the one hand there is no evidence that sister nuclei ever become conjugate in this simple way, and on the other hand, it has been shown in several cases that the two nuclei in the sporidium are *not* conjugate, but are merely the result of a precocious nuclear division to be followed later by a cell-division which leads to their separation (see discussion in earlier paper, (1) p. 354). It is much more probable that the conjugate condition is produced soon after infection by nuclear migration, or cell-fusion, between vegetative cells.

UROMYCES FICARIAE, Lév.

In this *micro*-form (which, however, sometimes exhibits a few uredospores among the teleutospores), Sapin-Trouffy describes the hyphae generally as being binucleate, so that it would appear to belong to the same category as the two forms just described. The form is not a favourable one for investigation, but from our observations the general mycelium appears to exhibit *single* nuclei, but the mass of mycelial hyphae round about the teleutospore sorus, as well as those directly connected with teleutospore formation, appear to have *conjugate* nuclei (Fig. 26). Thus the haustorium in a host-cell close to the teleutospore mass shows clearly two nuclei (Fig. 27).

Though it is difficult to make sure on this point, it is probable that we have in this form a condition somewhat intermediate between that of *Puccinia Malvacearum* and *P. Adoxae*; for while the conjugate nuclei appear to arise only in connexion with the teleutospores, yet they arise earlier than in the first-mentioned form, and produce a general mycelium of which part is vegetative and part only teleutospore-forming.

The existence of young teleutospores with three nuclei (Fig. 26), in this form, also suggests that the transition to the conjugate nuclear condition has only just taken place. Cells with abnormal numbers of

nuclei were not to be seen in *Puccinia Adoxae* and *Uromyces Scillarum*, and, as far as observations go, seem only to occur in connexion with such a transition process.

General Conclusions.

The conjugate nuclear condition of the fertile cells (basidia of older authors) of the aecidium is mainly the result of one of two processes. In the one case, there is a process of nuclear migration from a vegetative cell into a fertile cell (female cell); this has been observed in *Uromyces Poae* and *Puccinia Poarum*, as well as in *Phragmidium violaceum*, where it was first described (1). In the other case the fertile cells fuse in pairs, and thus the conjugate nuclear condition arises; this process was first observed by Christman (4) in *Phragmidium speciosum*, *Caeoma nitens*, and *Uromyces Caladii*, and is described for *Melampsora Rostrupi* in the present paper.

These two processes are to be considered as merely two different types of *reduced fertilization* which have replaced the normal fertilization in the absence of the normal male cells (spermatia). In the one case the female cell fuses (partially) with a vegetative cell, in the other case two female cells fuse together (vide supra, p. 86).

While in *U. Poae* nuclear migration seems to take place only into the fertile cells of the aecidium, in *Puc. Poarum* a small number of migrations appear to take place between vegetative hyphae also, either below the layer of fertile cells or before such cells have become differentiated. The conjugate nuclear condition in these cases is thus started before the differentiation of the cells which represent the female cells.

The *basal cells* of the aecidium may thus arise by the fertilization of a fertile (female) cell by a vegetative cell, by the conjugation of two fertile (female) cells or (rarely) as the product of an undifferentiated vegetative cell which has earlier undergone a process of fertilization.

This condition, described in the case of *Puc. Poarum*, leads on very easily to that found in *Puc. Malvacearum*, where there are no female cells, and the change to the conjugate nuclear condition takes place at a different point in the life-cycle, without the development of any specially differentiated structures, being found only in connexion with the vegetative hyphae, just before the formation of the teleutospores. From this point it is a short step to the condition found in other forms (*Puccinia Adoxae*, *Uromyces Scillarum*), where the simple and reduced fertilization process takes place at some earlier point in the life-cycle without apparent relation to the development of the teleutospores.

It is easy to understand that directly the primitive and 'external'

fertilization by means of spermatia was replaced by a simpler 'internal' fertilization, there would no longer be any bar to the shifting of the reduced sexual process to another point in the life-history. The Uredineae would appear to be a group in which the exact point at which the reduced sexual process (that has replaced in phylogeny the normal one) occurs is not perfectly fixed; though when the homologues of the female cells are present it mainly takes place in connexion with them. The fertilization, however, always occurs before the formation of the first spore-form after the sporidia, so that aecidiospores, uredospores, and teleutospores always show conjugate nuclei.

It is possible that an aecidium-bearing form may be found in which the nuclei become conjugate before aecidium formation, so that all the fertile cells will be binucleate from their first origin; such a case will only be an exaggeration of the condition found in *Puccinia Poarum*.

Investigation of the typical aecidium confirms the view put forward earlier (1) that it, like the simpler aecidium (caeoma), is to be considered as a sorus of female reproductive organs; in which, however, the outer layers of spores or spore-mother-cells have become sterilized to form the pseudoperidium.

The function of the pseudoperidium is, no doubt, protective, and its development in the typical aecidium is probably related to the deeper point of origin of that structure as compared with the sub-epidermal origin of the caeoma. The latter is to be considered as the more primitive type from which the typical aecidium has been derived.

A study of the reduced forms without aecidia shows clearly that these forms also exhibit an alternation of generations. The transition from the gametophyte to the sporophyte is, however, obscured in these forms owing to the fact that it takes place in an *apogamous*[1] way. The exact nature of the apogamy is yet unknown, but it is obviously the result of the interaction of undifferentiated vegetative cells or nuclei; and is a further stage of reduction of the process observed in the aecidium. In the reduced forms also the point of the life-cycle at which it occurs is not exactly fixed.

The transition from the sporophyte to the gametophyte (i.e. reduction) is as clear in the reduced as in the other forms, for it takes place in the teleutospore, which is present in all forms except the very aberrant genus, *Endophyllum*.

The gametophyte stage with single nuclei may be very well marked even in the reduced forms, or it may be inconspicuous, as is the case in *Uromyces Scillarum* and *Puccinia Adoxae*, where possibly it consists of little more than the promycelium. This stage, however, always passes over into the

[1] The term apogamy is used for want of a better one, but it is hardly satisfactory when applied to cases in which there is a fusion or association of nuclei (2 A).

sporophytic stage with conjugate nuclei before the occurrence of spore formation.

The sporophyte stage, with its three kinds of spores, is always very well marked in the forms with the full life-cycle, but in forms like *Puccinia Malvacearum* it is represented only by a few generations of cells with conjugate nuclei.

The actual chromosome-reduction no doubt takes place during the first division in the promycelium, but as the fusion of nuclei in the

teleutospore is clearly the preliminary to reduction it is convenient to make that fusion the starting-point of the gametophyte.

In the *-opsis* forms, which are not indicated in the diagram above, the mycelium arising from the aecidiospores gives origin directly to teleutospores.

The Basidiomycetes have clearly the same general and cytological life-history as the *lepto-* and *micro-*forms among the Uredineae, as pointed out earlier (1). In this group neither the method nor the exact point

at which the conjugate condition arises has yet been made out, but according to some recent work of Miss Nichols[1] the point at which the transition takes place appears, in this group also, to be different for different forms.

A diagram is given to exhibit the general and cytological life-history of the various forms.

[1] Trans. Wiscon. Acad. Sci. xv, 1905. This paper has not yet been seen, but it is quoted by Harper in an important work (Sexual Reproduction and the Organization of the Nucleus in certain Mildews) which was received too late to allow of its being considered in the present article.

List of Papers.

1. Blackman, V. H.: On the Fertilization, Alternation of Generations, and general Cytology of the Uredineae. Ann. Bot., xviii, 1904, p. 323.
2. ——————: Congo-Red as a Stain for Uredineae. New Phytol., iv, 1905, p. 173.
2 A. ——————: On the Relation of Fertilization, 'Apogamy,' and 'Parthenogenesis.' New Phytol., iii, 1904, p. 149.
3. —————— and Fraser, H. C. I.: On the Sexuality and Development of the Ascocarp in *Humaria granulata*. Proc. Roy. Soc., Ser. B, lxxvii, 1906, in the press.
4. Christman, A. H.: Sexual Reproduction of the Rusts. Bot. Gaz., xxxix, 1905, p. 267.
5. Farmer, J. B., Moore, J. E., and Digby, L.: On the Cytology of Apogamy and Apospory. Proc. Roy. Soc., lxxi, 1903, p. 453.
6. Neumann, R.: Ueber die Entwickelungsgeschichte der Aecidien u. Spermogonien der Uredineen. Hedwigia, xxxiii, 1894, p. 346.
7. Richards, H. M.: On some points in the Development of Aecidia. Proc. Amer. Acad. of Arts and Sci., xxxi, 1896, p. 255.
8. Sapin-Trouffy, P.: Recherches histologiques sur la famille des Urédinées. Le Botaniste, 5e série, 1896, p. 59.

DESCRIPTION OF PLATES III AND IV.

Illustrating the paper by Mr. Blackman and Miss Fraser on the *Uredineae.*

Figs. 1–10. *Uromyces Poae.*

Fig. 1. Early stage of development of aecidium beneath a stoma; a group of empty hyphae is seen above, and a mass of hyphae with uninucleate cells below. × 620.

Fig. 2. Later stage of development in which a few of the uninucleate cells have become binucleate; a nuclear migration is visible on the left. × 530.

Figs. 3–6. Examples of nuclear migrations into fertile cells. × 1350.

Fig. 7. Aecidium just before it breaks through the epidermis; a few aecidiospores are already fully formed, the contents of which stain very deeply as if they had become disorganized. The yet unbroken pseudoperidium is very distinct. × 620.

Fig. 8. Nucleus of aecidiospore-mother-cell, showing chromatin reticulum. × 1900.

Figs. 9 *a–d.* Stages of conjugate division. × 1900.

Fig. 10. Spermatia. × 1900.

Figs. 11–16. *Puccinia Poarum.*

Fig. 11. View of the mass of hyphae forming young aecidium; only a small portion is drawn, starting from just below the epidermis (on the left) and reaching to the base of the mass (on the right). Cells with conjugate nuclei are visible at the base of the mass. × 1350.

Fig. 12. Migration into fertile cell. × 1350.

Fig. 13. Migration from vegetative cell into fertile cell above. × 1350.

Fig. 14. Migration between two ordinary hyphae. × 1350.

Fig. 15. Early stage of division of cell with three conjugate nuclei. The three chromatin masses on their simple spindles and the three nucleoli are clearly visible. × 1900.

Fig. 16. Later stage of division of cell with four conjugate nuclei. × 1900.

Figs. 17 and 18. *Melampsora Rostrupi.*

Fig. 17. Two aecidiospore forming cells of young aecidium. The left-hand cell shows the remains of the partition wall indicating its origin by fusion; above it is an aecidiospore-mother-cell in division. The right-hand cell has two sterile cells side by side above it, which also point to its origin by fusion. × 1350.

Fig. 18. Another aecidiospore-forming cell showing its origin by fusion; two layers of disorganizing cells are visible above the aecidiospore-mother-cell. × 1350.

Figs. 19–23. *Puccinia Malvacearum.*

Fig. 19. Uninucleate hyphae growing up beneath epidermis of host to form teleutospore mass. × 1350.

Fig. 20. Young teleutospore mass showing young undivided spores arising from a group of binucleate cells; a cell on the right is trinucleate. × 1350.

Fig. 21. Cell with conjugate nuclei giving origin to two teleutospores; the one on the right has already divided, that on the left is still unicellular. × 1350.

Fig. 22. Young trinucleate teleutospore arising from trinucleate cell; the cell below also shows three nuclei. × 1350.

Fig. 23. Young trinucleate teleutospore before division. × 1350.

Figs. 24 and 25. *Puccinia Adoxae.*

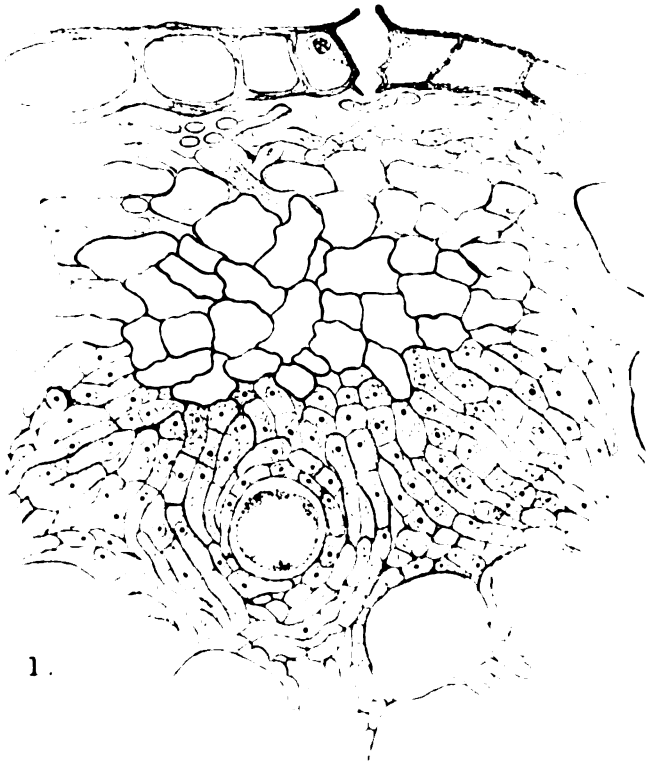
Fig. 24. View of young teleutospore mass showing the binucleate condition of both the teleutospores and the general mass of mycelium. × 430.

Fig. 25. Two vegetative hyphae showing the binucleate condition. × 1900.

Figs. 26 and 27. *Uromyces Ficariae.*

Fig. 26. Young teleutospore sorus developing beneath the epidermis; several of the teleutospores are trinucleate. × 430.

Fig. 27. Cell of host showing binucleate haustorium close to nucleus. × 1900.



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BLACKMAN AND FRASER — UREDINEÆ

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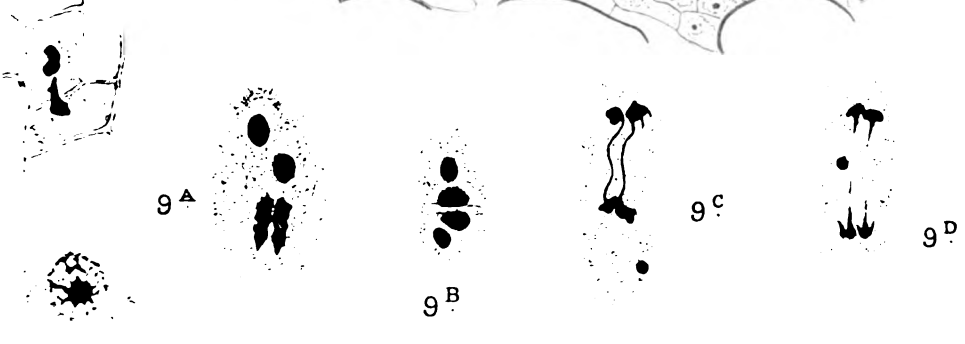
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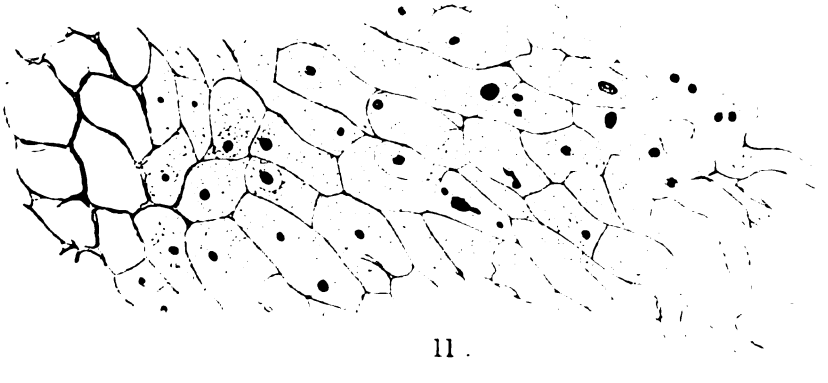
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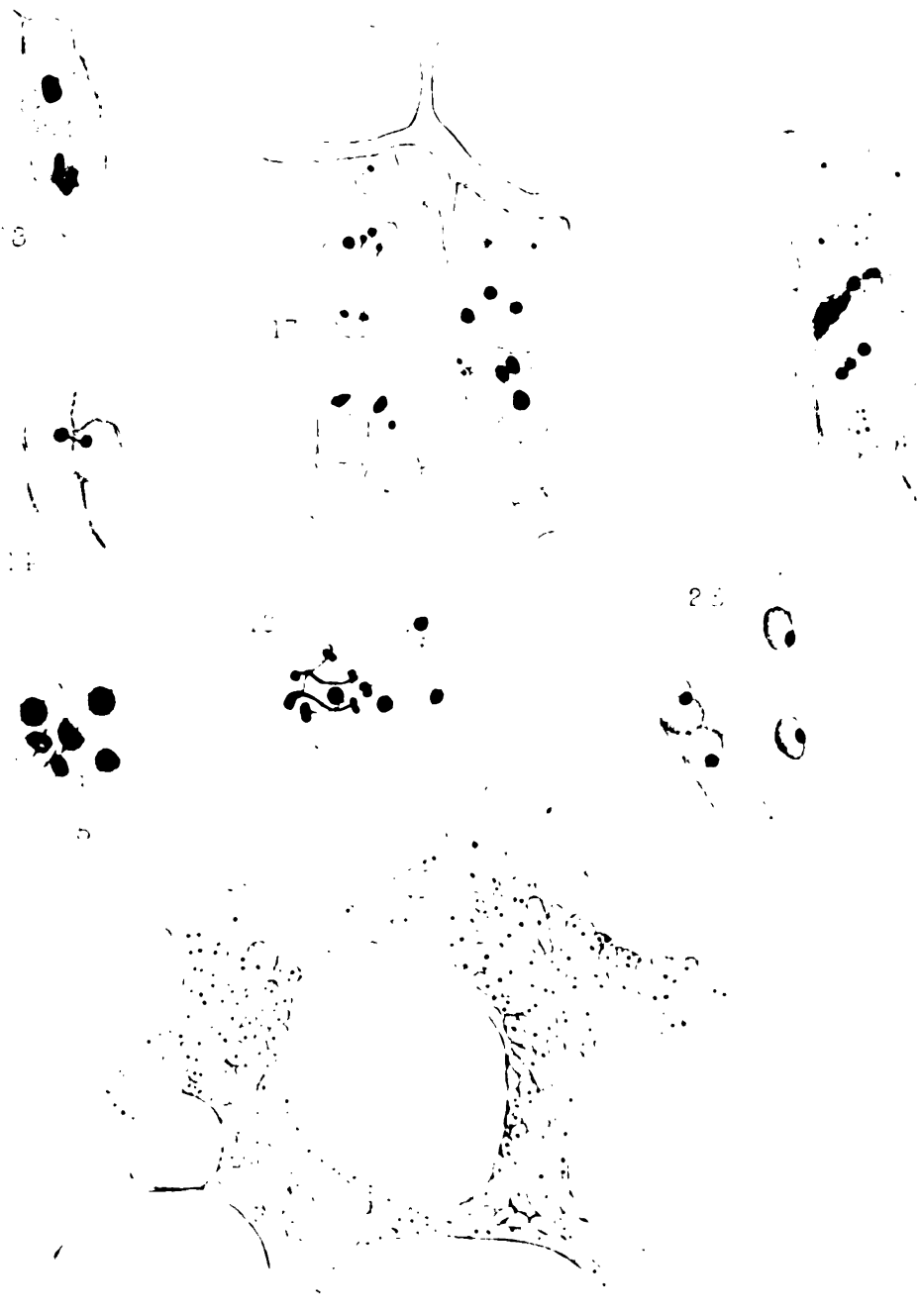

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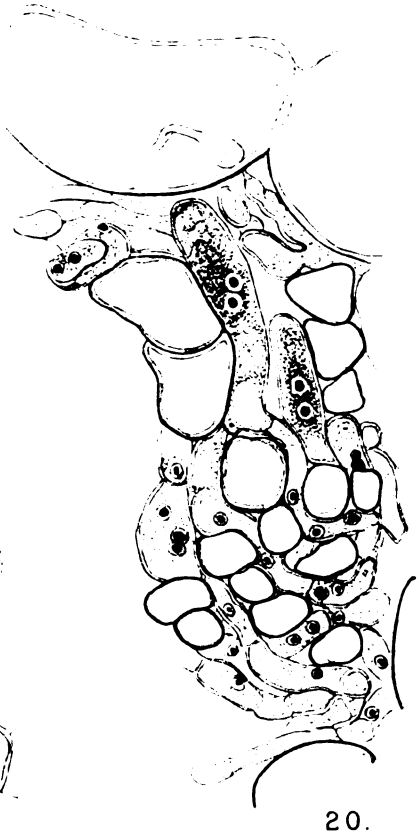

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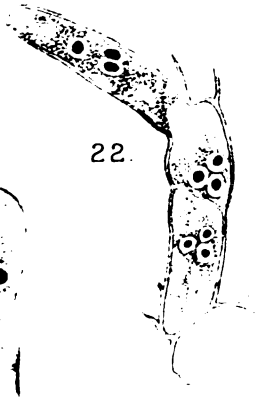

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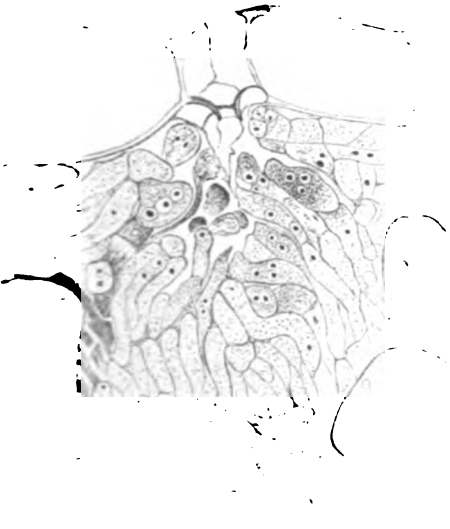

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Huth Lith^r London

The Enzymes of Polyporus squamosus, Huds.

BY

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FROM an anatomical study of wood undergoing decay through the agency of *Polyporus squamosus*, evidence was obtained that various enzymes are excreted by the Fungus [1]. Thus the disappearance of starch, proteids, and cellulose from the wood suggests that the mycelium produces amylolytic, proteolytic, and cytolytic enzymes. The experiments recorded in this paper were made partly with the object of supplementing these anatomical observations, and partly in order to increase our knowledge of the occurrence of enzymes in the Hymenomycetes. A number of investigations upon the enzymes of *Psalliota*, *Russula*, *Boletus*, &c., have been made by various observers [2], but little is known about those of the large tree-Fungi. Most of the latter belong to the genus *Polyporus*. Many of them are unsuitable for enzyme investigations owing to the tough or woody nature of their tissues. This, however, is not the case with *Polyporus sulphureus* and *Polyporus squamosus*. The former has bulky and very juicy fruit-bodies. Bourquelot and Hérissey [3] have taken advantage of this fact, and have given us an account of the enzymes present in them.

Polyporus squamosus is one of the largest and commonest of British Polyporei. Its ochraceous fruit-bodies, often a foot across and splashed with brown scales above, are frequently to be seen projecting in the form of brackets, either singly or several together, upon the Sycamore, the Horse-chestnut, the Elm, the Ash, and various other deciduous trees in woods, parks, and gardens. When the fruit-bodies are young they are soft and juicy, and an extract can be made from them with ease. This extract has been tested altogether for thirteen different enzymes. The investigation has afforded evidence that at least eight or nine are present in the fruit-bodies.

Fresh young fruit-bodies were obtained, as required, from a tree at the

[1] Buller, *Polyporus squamosus* as a timber-destroying Fungus, Journ. of Econ. Biol., vol. i, No. 2 (in the press), 1906.

[2] For literature see Reynolds Green, Fermentation, Cambridge, 1899.

[3] Bourquelot et Hérissey, Les ferments solubles de *Polyporus sulphureus*, Bull. de la Soc. Mycol. de France, t. x, 4e fasc., 1895, p. 235.

[Annals of Botany, Vol. XX. No. LXXVII. January, 1906.]

Botanical Gardens, Birmingham, and their juice extracted. The extract, except where stated otherwise, was made from living and sound fruit-bodies directly before each experiment. One hundred grams of the Fungus were cut up into thin slices and then pounded in a mortar with 100 c.c. water for about forty minutes. The mixture was filtered through a cloth, this being folded over the residue and twisted, so as to extract as much juice as possible. The amount of the extract from a given weight of a fruit-body was fairly constant. One example will suffice. From 100 gm. Fungus plus 100 c.c. water, 136 c.c. of liquid were extracted. The extract was light in colour and neutral in reaction.

(1) *Amylase* (*diastase*). In testing for this enzyme 1 c.c. of the extract was added to about 20 c.c. of a 5 per cent. solution of Lintner's soluble starch in a test-tube *a*. As a control experiment a similar mixture was made in a test-tube *b*, the extract, however, being first boiled. The tubes were kept at a temperature of 28° C.

After sixteen hours 5 c.c. of the solution in *a* was added to 5 c.c. of Fehling's solution and boiled for ten minutes. The Fehling's solution was thereby almost completely reduced, the blue colour practically disappearing and a large precipitate of cuprous oxide being thrown down. The control was tested in a similar manner when it was found that the colour of the Fehling's solution remained unchanged. Only the minutest trace of cuprous oxide was thrown down, doubtless due to some substance in the original extract, for this was found to have a very slight reducing action immediately after it was made. The complete hydrolysis of the starch in the test-tube *a* was confirmed by the gradual disappearance of the blue reaction on testing with iodine.

Bourquelot and Hérissey (loc. cit.) demonstrated the presence of diastase in *Polyporus sulphureus* so that it was almost to be expected that *Polyporus squamosus* would contain a similar enzyme.

(2) *Laccase.* To determine the presence of laccase, 5 c.c. of the extract was added to 10 c.c. of a 5 per cent. hydroquinone solution in a 50 c.c. flask *a* stoppered with cotton wool. A similar mixture was made as a control in a flask *b*, the extract, however, being first boiled. The flasks were kept at the temperature of the laboratory.

After three hours the liquid in flask *a* had assumed a distinct rose-tint and after eighteen hours was deep brownish red. During the next few days the colour gradually deepened. An iridescent pellicle consisting of green crystalline scales of quin-hydrone, with a metallic lustre, appeared on the surface of the fluid, and a dark red precipitate of the same substance was thrown down. There was a distinct smell of quinone. In the control the mixture was practically colourless after eighteen hours. Although within the next fourteen days the colour of the fluid darkened, no iridescent pellicle, dark red precipitate or smell of quinone was developed.

These experiments indicate that the fruit-bodies contain the oxydase called laccase.

(3) *Tyrosinase.* To 5 c.c. of the extract was added 10 c.c. of a saturated solution of tyrosin in a 50 c.c. flask *a*, stoppered with cotton wool. A control was made in the same manner in a flask *b*, the extract, however, being first boiled. The temperature was that of the laboratory. Toluol was used as an antiseptic.

At the end of sixteen hours the contents of flask *a* were found to have turned a deep black, and after thirty-six hours a very deep black. The control remained colourless.

As it seemed just possible that the black colour in the flask *a* might have been produced by the oxidation of some substance in the extract, and not of the tyrosin, a second control was made. To 5 c.c. of the extract was added 10 c.c. water in a flask *c*. After sixteen hours the mixture had turned brownish but not nearly so dark as that in flask *a*. By comparing this result with that obtained in *b* we may conclude that the extract contains some substance which on oxidation (probably by means of an oxydase) becomes dark coloured.

The above experiments indicate that the fruit-bodies contain the oxydase called tyrosinase.

(4) *Protease.* The Fungus extract was tested upon gelatine, fibrin, and Witte peptone. To a solution of 7 per cent. unneutralized gelatine in a test-tube *a*, 2 c.c. of the extract were added. A similar preparation was made as a control in a test-tube *b*, the extract, however, being first boiled. A spot of toluol was added to each tube. The temperature was that of the laboratory.

After twenty-two hours the jelly in *a* was found to be liquefied to a depth of 3 mm., and after thirty-two hours to 6 mm. No liquefaction occurred in the control.

Similar experiments were made with broth-gelatine containing 10 per cent. gelatine and 0·2 per cent. carbolic acid. There was a gradual liquefaction of the gelatine as a result of the action of the extract. In the control no liquefaction took place.

When pure cultures of the mycelium were made upon malt-wort extract solidified with 10 per cent. gelatine gradual liquefaction of the latter took place.

The above experiments leave no doubt that *Polyporus squamosus* produces an enzyme which liquefies gelatine.

Since the exact chemical nature of gelatine does not seem to be very clear, it was thought well to test the Fungus extract upon such undoubted proteids as fibrin and Witte peptone.

Upon fibrin the extract appeared to have no digestive action whatever. Ten grams of the dried Fungus chips were extracted with 100 c.c. water.

The extract was added to fibrin in test-tubes. The latter were then shaken up and set in a warm bath at 40° C. After two days the fibrin had undergone no apparent digestion. The following table gives fuller details of the experiment.

TABLE I.

	No.	*Extract.*	*Fibrin.*	*Antiseptic.*	*Acid or alkali added.*	*Special treatment.*	*Result.*
Experiment	1	20 c.c.	0·5 gm.	0·25 c.c. toluol	none	—	Fibrin not apparently digested after 48 hours
Control	2	,,	,,	,,	,,	extract boiled.	
Experiment	3	10 c.c.	0·5 gm.	0·25 c.c. toluol	5 c.c. of a 0·5 per cent. sodium carbonate solution.	—	
Experiment	4	,,	,,	,,		—	
Control	5	,,	,,	,,		extract boiled.	
Experiment	6	10 c.c.	0·5 gm.	0·25 c.c. toluol	5 c.c. of a 0·2 per cent. hydrochloric acid solution.	—	
Experiment	7	,,	,,	,,		—	
Control	8	5 c.c.	0·25 gm.	0·125 c.c. toluol	one half the above amount.	extract boiled.	

According to Vines[1] a certain vegetable protease is so constituted that, whilst it is unable to break down the albumens, it yet has the power to bring about the hydrolysis of albumoses and peptones. Such an enzyme he calls erepsin. The extract of *Polyporus squamosus* appears to act in this way. The tests for hydrolysis were made upon Witte peptone in Nessler tubes at a temperature of 40° C. in accordance with the methods of Vines. The following table gives particulars of the experiments.

TABLE II.

	No.	*Fungus.*	*Witte peptone.*	*Special treatment.*	*Results with iodine after*	
					15 *hours.*	39 *hours.*
Experiment	1	extract from 2 gm. of dried Fungus chips made up to 50 c.c. with water.	0·3 gm.	1·5 c.c. of a 4 per cent. hydrocyanic acid solution.	distinct violet ring.	well-marked violet ring.
Experiment	2		,,	none.	,,	very distinct violet ring.
Control . .	3		,,	extract boiled.	no violet colour.	no violet colour.
Experiment	4	2 gm. of dried Fungus chips to which were added 50 c.c. of water.	0·3 gm.	1·5 c.c. of a 4 per cent. hydrocyanic acid solution.	violet precipitate.	very distinct violet precipitate.
Experiment	5		,,	none.	,,	,,
Control . .	6		,,	Fungus chips boiled.	no violet precipitate.	no violet precipitate.

[1] The Proteases of Plants, Ann. of Bot., vol. xix, 1905, pp. 171–87.

The results in the above table indicate that the Fungus extract is capable of breaking down Witte peptone so that the products give the reaction for tryptophane. We may therefore conclude that the Fungus extract contains a protease which, according to Vines, may be considered to be an erepsin.

Bourquelot and Hérissey (loc. cit.) found a feebly proteolytic enzyme in *Polyporus sulphureus*. In respect to this enzyme, then, *Polyporus squamosus* behaves similarly.

(5) *Emulsin.*

TABLE III.

	No.	*Extract.*	*Amygdalin 5 per cent.*	*Antiseptic.*	*Prussian blue reaction after*		*Smell after 40 hours.*
					23 hours.	*40 hours.*	
Experiment	1	1 c.c.	5 c.c.	toluol	distinct green	distinct green followed by a blue precipitate.	strong of HCN and benzoic aldehyd.
Experiment	2	1 c.c.	5 c.c.	benzene	very faint green	faint green followed by light blue precipitate.	distinctly of HCN and benzoic aldehyd.
Control. .	3	1 c.c. boiled.	5 c.c.	toluol	yellow	yellow: no trace of blue.	none.

The particulars of the experiments, made in test-tubes at about 18° C are embodied in the above table. The Prussian blue and smell tests clearly indicate that the fruit-bodies contain an emulsin enzyme.

(6) *Rennetase.* To 10 c.c. of fresh milk 2 c.c. of Fungus extract were added in a test-tube *a*. The control was made in a similar manner, the extract, however, being first boiled. The tubes were placed at a temperature of 28° C.

After forty-five minutes the contents in *a* had coagulated, whereas in the control there was no coagulation at all.

A few grams of a fruit-body, which had been carefully dried in thin slices, were pounded up with water and sand. The extract was forced through a cloth. Similar experiments to those just described were then made.

Clotting of the milk was seen to have begun fifteen minutes after the beginning of the experiment. At the end of two hours there was a solid plug at the top of the tube. The control remained unclotted.

The above experiments clearly prove that the fruit-bodies contain a rennetase.

(7) *Lipase.* The extract from 100 gm. of the Fungus pounded up with 100 c.c. water was 164 c.c. The tests were made upon a solution of 1·84 per cent. ethyl acetate. The 50 c.c. flasks employed were corked and placed in

a warm chamber at 28° C. Litmus solution was used for determining neutrality. The other details of the experiments are given in the table.

TABLE IV.

	Acetate solution.	*Extract*	*Toluol.*	*Amount of $\frac{1}{10}$ normal KHO solution in c.c. required for neutralizing 10 c.c. after*			
				40 hours	*51 hours.*	*93 hours.*	*330 hours.*
Experiment	40 c.c.	10 c.c.	0·5 c.c.	3·8	11.06	15·5	18·4
Control	40 c.c.	10 c.c., boiled	0·5 c.c.	0·14	0.12	0·15	0·3
				after 40 hours.	*after 51 hours.*	*after 93 hours.*	*after 330 hours.*
Excess KHO in experiment over control by subtraction				3.66	10·94	15·35	18·1
Grams of ethyl acetate hydrolyzed in 10 c.c. by calculation				0·0161	0·0481	0·0631	0·0796

It is evident from the results given in the above table that the ethyl acetate underwent continual hydrolyzation, 43 per cent. thus becoming split up in 330 hours. In the control there was practically no hydrolyzation. The presence of a lipase in the Fungus extract is thus made highly probable. It must not be forgotten, however, that a lipase is an enzyme, which splits up fats, and not necessarily such esters as ethyl acetate. It is as yet not absolutely certain that such an alcohol as ethylic can replace glycerine in the molecule so as to be acted upon in the same manner by lipase. Provisionally, however, it seems to me best to retain the name lipase for those enzymes which have the power of splitting up such compounds as ethyl acetate.

It may here be mentioned that when spores of *Polyporus squamosus* are allowed to dry for several days, many of them develop large fat-drops. On germination of the spores in malt-wort extract these drops disappear. Perhaps this is due to the action of a lipase.

(8) *Pectase.* The juice was squeezed out of fresh, ripe, red currants, filtered, then boiled and refiltered. Excess of alcohol was added to precipitate the pectin. This was then filtered as dry as possible with the aid of a suction filter. Water was then added to dissolve the pectin and the solution placed on a warm bath to drive off the alcohol. This solution was then used in testing for pectase.

The following were preliminary experiments to assure myself that the solution contained pectin. To 1 c.c. freshly extracted carrot-juice, which is known to contain pectase, 5 c.c. of the pectin solution were added in a

porcelain dish *a*. In a control experiment, made similarly, 1 c.c. of water was used instead of the carrot-juice.

After five hours the contents of the dish *a* had clotted into a single lump whereas the control remained unchanged. The experiments indicate that the solution prepared from the currants does contain pectin which can be clotted by pectase.

Experiments were then made with the extract of *Polyporus squamosus*. Of the pectin solution 25 c.c. were neutralized with $\frac{1}{20}$ normal potassium hydroxide solution and a few drops of a calcium chloride solution added. To 5 c.c. of the resulting solution 1 c.c. of the fresh *Polyporus* extract was added in a porcelain dish. A control was made in a similar manner, the *Polyporus* extract, however, being first boiled.

The result was negative. During the course of several days no clotting whatever occurred.

It was then thought that a pectase might possibly be present in the fresh Fungus in such a manner as not to be easily extracted, whereas it might be obtained from fruit-bodies which had undergone desiccation. Slices of the fresh Fungus were therefore dried over sulphuric acid *in vacuo*. The dry chips were then pounded up with water and an extract obtained. Experiments similar to those described with the extract from the undried *Polyporus* were then made.

The results were again entirely negative. No clotting occurred. In a control experiment made at the same time, in which carrot-juice was used instead of the *Polyporus* extract, clotting began in the course of two hours and was completed in 3·5 hours.

The above experiments leave little doubt that the fruit-bodies of *Polyporus squamosus* do not contain a pectase enzyme.

(9) *Invertase*. To 50 c.c. of a 5 per cent. solution of cane-sugar 5 c.c. of the Fungus extract were added in a test-tube *a*. A drop of toluol was used as an antiseptic. A control was made in a similar manner in a test-tube *b*, the extract, however, being first boiled. Both tubes were placed at a temperature of 29° C.

After twenty-four hours 5 c.c. from each tube were boiled with 5 c.c. freshly made Fehling's solution. In each case there was a very slight reduction of copper sulphate.

After forty-eight hours the same test was again tried and a similar result obtained. There was only a very slight precipitate in each case, thus indicating that the extract had not brought about any inversion of the cane-sugar.

Similar experiments were made with an extract from carefully dried chips of the fruit-bodies. The results, however, were again negative.

The above experiments leave little doubt that the fruit-bodies do not contain invertase. Here, again, the conditions are similar to those in *Poly-*

porus sulphureus, for Bourquelot and Hérissey (loc. cit.) were unable to detect the enzyme in that species.

(10) *Maltase.* One gram of dried slices of the Fungus were well rubbed up with sand and a little of a 2 per cent. maltose solution. Of this mixture half by weight was put into each of two 100 c.c. flasks which were then filled up to the 100 c.c. mark with 2 per cent. maltose. The contents of one flask were boiled in order to make a control experiment. One c.c. toluol was used as an antiseptic in each case. The flasks were placed in a warm chamber at 29° C.

At the end of three days 25 c.c. were removed from each flask, mixed with aluminium hydrate, and then filtered. The clear solutions thus obtained were then tested in the polarimeter. The readings were almost identical.

The experiments indicate that the fruit-bodies do not contain maltase.

(11) *Trehalase.* Some trehala manna was obtained for me by Professor Adrian Brown through the kindness of the Pharmaceutical Society. From the manna a small amount of trehalose was prepared. The Fungus extract was made by rubbing up 5 grams of the dried fruit-bodies with 50 c.c. of water.

To 10 c.c. of a 3 per cent. trehalose solution 1 c.c. of extract was added. A polariscope reading was then taken. Further polariscope readings were taken at intervals for three days, but no change was observed. The experiment, therefore, seems to indicate that no trehalase is present in the Fungus extract. However, Bourquelot and Hérissey (loc. cit.) found that this enzyme is present in the fruit-bodies of *Polyporus sulphureus*. It is, therefore, somewhat surprising that *Polyporus squamosus* does not seem to contain it.

(12) *Cytase.* As a preliminary experiment and control 20 gm. of oats, which are known to contain cytase, were ground up, mixed with water, and after two hours filtered. The extract was then allowed to act on thin sections of barley-grains which had been cleared of starch in the course of twenty-four hours by means of saliva. The sections were watched in hanging drops under the microscope[1]. After two hours the cellulose walls of the sections were seen to be swelling and dissolving away, proving that a cytase had been extracted from the oats.

Similar experiments were made with a *Polyporus* extract, but with negative results, so that I was unable to prove the presence of a cytase in the fruit-bodies. Owing to the disappearance of cellulose from the walls of the cells in the wood of the Sycamore under the action of the Fungus[2] there can, however, be little doubt that the vegetative part at least produces abundant cytase.

(13) '*Coagulase.*' According to the recent work of Wolff and

[1] See Marshall Ward, A Lily Disease, Ann. of Bot., vol. ii, 1888. [2] Buller, loc. cit.

Fernbach [1], malt contains an enzyme capable of causing the precipitation of starch from solution. It seemed to me of interest to test for the supposed new enzyme in the Fungus extract.

Ten grams of some dried chips of fruit-bodies were ground up with 100 c.c. water and an extract made. Soluble starch was then prepared by gelatinizing 50 gm. potato starch in 1000 c.c. boiling water and by then subjecting the mixture to a pressure of about two atmospheres for two hours in an autoclave. The experiments were made in tall 50 c.c. glass jars.

TABLE V.

	No.	Soluble starch in c.c.	Extract in c.c.	Toluol in c.c.	Result after		Iodine reaction of clear solution after	
					1 hr.	20 hrs.	20 hrs.	70 hrs.
Experiments.	1	50	1	0·5	no change	no precipitate	blue	violet
	2	50	3	0·5		precipitate about 1 in. high	violet	red
	3	50	10	0·5		dense precipitate nearly to top of jar	red	red
Controls. Extract boiled.	4	50	1	0·5	no change	no precipitate	blue	blue
	5	50	3	0·5		no precipitate	blue	blue
	6	50	10	0·5		no precipitate	blue	blue

The above table gives an account of the experiments and the results. The white precipitate produced as a result of the action of the extract on the soluble starch gradually settled down, leaving a clear solution above. The precipitate, which under the microscope was found to consist of small particles, stained a deep blue with iodine. Exactly similar results were obtained in a set of experiments made like those described in the table but without the use of toluol. These results closely agree with those obtained in some preliminary experiments by acting upon soluble starch with malt extract under the conditions employed by Wolff and Fernbach [2]. If the starch precipitate is due to a special enzyme, coagulase, there is, therefore, reason to believe that the latter is present in the Fungus extract.

The clear solution above the starch precipitate was tested with iodine. In the course of the experiments the clear solution was found

[1] Wolff u. Fernbach, Compt. rend., Nov. 2, 1903. [2] loc. cit.

to change its reaction gradually from blue to red, indicating the formation of erythro-dextrin. We thus have another proof of the presence of an amylase in the extract.

(14) *Hadromase.* According to Czapek, *Merulius lacrimans* and certain other wood-destroying Fungi produce an enzyme which he has called hadromase, and which is capable of splitting hadromal from cellulose [1]. He regards these bodies as being united in an ether-like compound in lignified membranes [2].

In the case of *Merulius lacrimans* the hadromal does not appear to be destroyed, for it can be dissolved out of rotted wood with alcohol, &c., in considerable quantities after the cellulose has practically disappeared. On the other hand, I found it impossible to extract hadromal in this way from the sawdust of the wood of *Acer pseudoplatanus* which had been rotted by *Polyporus squamosus.* The tests for hadromal were made with phloroglucin. If the mycelium in the wood-cells produces hadromase it seems likely that the hadromal split off from the cellulose becomes immediately destroyed by some further chemical process.

The extract of the fruit-bodies was not tested for hadromase, but a study of the wood of *Acer pseudoplatanus*, which was being rotted by the mycelium of the Fungus, showed that some of the fibres were undergoing 'delignification' or that the walls were becoming so altered as to take on the reactions for cellulose with chlorzinc iodine [3]. Further, the hyphae had made numerous holes in the lignified cell-walls. It seems, therefore, not unlikely that the mycelium produces hadromase. One could scarcely expect it to occur in the fruit-bodies.

Thin slices of the fruit-bodies were carefully dried at a temperature of about 80° C. and preserved in a well-stoppered bottle. After nine months, tests were again made for some of the enzymes. The extract from this preserved material appeared to be just as active as that made from the same material when it was first dried. Thus milk was clotted in fifteen minutes, an 0·2 per cent. Lintner's starch solution underwent complete hydrolysis in three hours, and gelatine was liquefied about as rapidly as in the first experiments. I have, therefore, found the material well suited for experiments by students in the laboratory.

Kohnstamm [4] states that he found an amylase, emulsin, and a protease in the fruit-bodies of *Polyporus squamosus.* His material, however, was

[1] Czapek, Zur Biologie der holzbewohnenden Pilze, Ber. d. D. Bot. Gesell., Bd. xvii, 1899, p. 166.

[2] Czapek, Ueber die sogenannten Ligninreactionen des Holzes. Zeitschrift für physiologische Chemie, Bd. xxvii, 1899, p. 14.

[3] Buller, loc. cit.

[4] Amylolytische, glycosidspaltende, proteolytische und Cellulose-losende Fermente in holzbewohnenden Pilzen. Beih. z. Bot. Centralbl., Bd. x, 1901, p. 90.

collected in January and March. As fruit-bodies which have hung on trees through the winter are always dead and usually worm-eaten and attacked by saprophytic Fungi, a confirmation of his results with fresh and perfectly sound material, as given in this paper, seemed to me highly desirable.

My work has shown that the following enzymes occur in the fruit-bodies of *Polyporus squamosus*: laccase, tyrosinase, amylase, emulsin, a protease, lipase, rennetase, and 'coagulase'; whereas negative results were obtained in the tests for pectase, maltase, invertase, trehalase, and cytase. A study of the destruction of the wood of the Sycamore (*Acer pseudoplatanus*[1]) points to the conclusion that the mycelium produces cytase and possibly also hadromase. Altogether, then, we may take it that the Fungus produces eight or nine different enzymes. Whether a greater number of these bodies has been proved to be present in any other single organism is doubtful. However, seven have been shown to exist in *Aspergillus* by Bourquelot[2], namely, invertase, maltase, trehalase, inulase, emulsin, diastase, and trypsin.

The more we know of physiology the more important do enzymes appear to be in the metabolism of living organisms. Doubtless beyond the eight or nine enzymes found in *Polyporus squamosus* there are others present with which we are not yet acquainted. The absence of invertase, maltase, and trehalase suggests that some other corresponding enzyme is still to be detected. In any case a sufficient number of enzymes have been recorded to give us some insight into the great complexity of the chemical processes going on in the fruit-bodies.

In conclusion I wish to express my best thanks to Professor Adrian Brown for permitting me to carry out this investigation in the Brewing Department of the University of Birmingham, and for valuable advice in connexion with the tests for the enzymes.

[1] Buller, loc. cit.

[2] Bull. Soc. Mycol., 1893, p. 231.

The Incapacity of the Date Endosperm for Self-Digestion.

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INTRODUCTION.

THAT the digestion of nourishment stored in the endosperm is accomplished by the influence of enzymes which are secreted, or at least become active under conditions of germination, is universally accepted. The results and conclusions of various investigators are by no means uniform, as to whether or not the enzymes are developed in the embryo only or also in the endosperm independently of the embryo. The prevailing opinion, as recognized by Pfeffer, is that the endosperms of many grasses, palms, &c., possess a capacity for auto-digestion; that is, that such endosperms from which the embryos have been removed will, under optimum conditions of germination, provided digestion products may easily escape, digest themselves and become depleted of their storage substance. This view has become so widely accepted as no longer to be questioned.

When one examines the evidence upon which this conclusion rests he is surprised at its weakness. Moreover, associated with this view is a conception which is wholly out of date. The various authors have regarded as an almost self-evident fact that digestion by enzymes is evidence of vitality. The idea that a given tissue which happens to contain something capable of doing enzyme work is to be regarded as living matter, is no longer modern.

This paper is intended to show, first: that the literature as it stands does not furnish convincing proof of auto-digestion by endosperms, and second, that the date endosperm which Puriewitsch found to be capable of auto-depletion, and which he regards as living matter, does not possess such capacity.

The weakness of the evidence as presented by various authors is in nearly every case to be explained by unreliable data. For instance, the seeds have been allowed to germinate before removing the embryo when

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it is well known that the latter contains enzyme. Some have based conclusions on the fact that the 'culture fluid' reduced Fehling's solution. The latter is of no significance unless it be known that reducing substances are not already present in the endosperm.

It is of course essential to understand what constitutes auto-depletion. The mere diffusion of soluble cell-substance from the tissue cannot be regarded as such. There must be evidence of chemical change, such as corrosion of starch-grains or dissolution of cell-wall. That the storage organs in some seeds are the cotyledons must not be overlooked, and the distinction must always be made between the behaviour of fleshy embryos and endosperms.

Historical.

Gris ('64, p. 90), in a notable contribution to the anatomy and physiology of germination, mentions some changes which were observed in the cell contents (aleurone especially) during germination, but Van Tieghem was the first to attack the problem directly. Van Tieghem ('77, p. 582) found that isolated endosperms of *Ricinus communis* under germination respire and are self-digesting, since the aleurone and oil are consumed, while the endosperms of *Canna* (amylaceous) and date (horny) are 'passive' and remain unchanged. He clearly implies that endosperms rich in oil and aleurone are self-digesting and possess vitality, while starchy endosperms and those containing reserve cellulose are not self-digesting and do not possess vitality. This conclusion rests purely on microscopical observations, and while the changes observed in *Ricinus* do indicate self-digestion, the possibility of a feeble digestion by the date is not excluded by such observations. So far as I am aware, this conclusion of Van Tieghem's regarding *Ricinus* has never been questioned.

Green ('90, p. 146) investigated the germination of *Ricinus communis* and found a 'ferment to exist as zymogen in the resting seed which is readily developed by warmth and weak acids into an active condition.' As to the relative influence of the endosperm and embryo he found 'the changes to be initiated in the endosperm, for they take place, although more slowly when the embryo is carefully removed.' The changes referred to consist (Green, '90, p. 147) in the saponification of fat into glycerine and ricinoleic acid especially, also the formation of sugar. Unfortunately the details of this work are not sufficient to permit any judgement as to the degree of demonstration attained.

Green ('86, p. 57) made glycerine extracts of the cotyledons of date-seedlings and of the endosperm-residue. Both extracts were applied to ground endosperms of resting date-seeds, but neither gave evidence of hydrolytic activity. We do not know what evidence was searched for, as the author merely states that, 'after prolonged action neither of them

(extracts) seemed to have had any effect, at least the quantity of ground cellulose had not apparently diminished.' However, another portion of the cotyledon extract was found by Fehling's test to have formed reducing sugar by its action on manufactured cotton fibre, while a similar portion boiled to destroy the enzyme was found to have no action on cotton fibre. From these results, and an examination of the cotyledon-structure, Green concludes that the ferment exists only in the epidermal cells of the cotyledon, and since the endosperm extract seemed to yield no sugar after contact with the ground resting endosperms, he finally says regarding the endosperm, 'there was no evidence that the extract of the endosperm had any action on cellulose at all. Evidently in it there is no ferment and the change is due to agencies quite external to its cells.'

Brown and Morris, after an extended study of the barley endosperm, agreed with Van Tieghem that the amylaceous endosperm of the grasses is a 'dead store house' of reserve material. In the same paper ('90, p. 480) the possibility is left open that the aleurone layer may contain some residual vitality, but the starch-bearing cells do not, and the conclusion including the 'dead store house' applies only to these starch-grain-cells. They further found ('90, p. 525) that the diastatic capacity of scutellum-cells is destroyed by treatment with vapour of chloroform. But when 'portions of the integuments of germinating barley, with their adherent aleurone layer, are treated in a similar way with chloroform vapour, we have found that their diastatic power *is not in the least impaired*, the starch under such sections being as quickly and completely attacked as under sections which have not been treated. Moreover, we have observed the same thing even after the fragments have been immersed for some time in absolute alcohol.' These authors assume that such treatment must have destroyed vitality, yet they acknowledge that the diastatic capacity remains undiminished. If then diastatic activity can proceed in dead tissue, how did these authors conclude that the amylaceous tissue of the endosperm constitutes a 'dead store house' because it does not possess diastatic activity? The inference of course is, that if such cells had been found able to do enzyme work they would have been regarded as living. As a matter of fact, their conclusion is that the aleurone cells are living because they show diastatic activity, and yet this activity was manifested under conditions which must have prohibited vitality. This affords an excellent example of the trouble which arises when vitality and enzyme activity are confused. It must be said here that these authors probably do not hold such views at the present time, but in a review of this kind it is necessary to deal with the literature as it stands. They further find ('90, p. 509) that translocation diastase is probably produced in the endosperm-cells by the embryo during its ante-resting development and that residual translocation diastase constitutes the diastase of the resting

grain. It may be said in this connexion that no one has proved that the diastase of the resting grain is in the endosperm as well as in the embryo. They do show ('90, p. 507) that during formation of the seed the diastase increases. The proportion of diastase was estimated at three stages, namely: endosperm about one half developed, endosperm about two-thirds developed, endosperm fully developed but not ripe. This does not show, however, as stated by Green ('01, p. 18), that the increase of enzyme takes place in the endosperm unless we assume that during the early development the embryo is too small to be considered. Brown and Morris do not state that they estimated the diastase present in the endosperm, but that they estimated the diastase in the grain when the endosperm was in varying stages of maturity. In this connexion they also state that a similar quantity of mature ungerminated grains yielded a similar quantity of cupric oxide. In this later test, however, the ungerminated seeds were allowed to steep, just how long is not stated, nor at what temperature, but if as long as in a preceding experiment (p. 496) the steeping lasted 24 hours and the temperature was not high enough to kill the embryo. Even if the steeping were only twenty-four hours the possibility of enzyme passing from the embryo to the endosperm is open[1]. On p. 507, they show that the major part of the soluble enzyme in the resting seed (after steeping) is located in the proximal half (embryo half), and that some also exists in the distal half. If it were not for the steeping a demonstration of enzyme in this distal half would be conceded. This paper of Brown and Morris may then be summarized as attributing diastatic capacity and vitality to the aleurone cells but as denying both to the amylaceous endosperm.

Grüss ('93, p. 288) found evidence of enzyme activity in the endosperm of maize from seedlings whose hypocotyls had elongated to six or seven centimeters. Since the aleurone layer and scutellum contain a much greater quantity of enzyme, he concluded that the diastase is secreted by these tissues and by diffusion from them penetrates the endosperm. Later, Grüss ('96, p. 439) found that isolated endosperms of maize under sterile conditions of germination for twelve days gave a very positive reaction with the guaiac-hydrogen-peroxide test. A similar result was obtained with the endosperm of barley. If this guaiac test is to be accepted as reliable we must regard the capacity of the endosperms of maize and barley to generate enzyme independently of the embryo as demonstrated. To support this by further evidence the direct sugar test was made with Fehling's solution. In this case, the barley endosperms were in moist sand four days, but no statement is made that sterile conditions were maintained. The glycerine extract from these endosperms after digestion for eighteen

[1] Brown and Escombe ('98, p. 11) concede the possibility of enzyme from the embryo penetrating the endosperm during steeping, and say that the embryo should be removed while the seed is still dry.

hours with 1 per cent. starch-paste and diluted gave a mixed solution 5 cc. of which reduced 1·8 cc. of Fehling's solution. A similar solution from normally germinated seeds reduced 1·9 cc., while such a solution from ungerminated seeds reduced 1·1 cc. This experiment is not conclusive, for the following reasons :—It is not positively stated or implied that the endosperms remained sterile; the starch-paste may have contained a little sugar; the digestion during eighteen hours may not have been free from the influence of organisms, as no statement of such precaution is made; ten hours is the limit of safety without antiseptics at 37° C.; the end reaction with Fehling's solution is not accurate to even 1 cc. with mixed solutions containing proteid and starch in varying stages of alteration; the small differences of ·1 cc. between the reducing power of the solution from isolated endosperms and of the solution from normally germinated seeds is suspicious. Moreover, if the endosperm contains reducing substance an extract from material soaked four days would probably contain more of such reducing substance than a similar extract from dry resting endosperms even though the time of extraction in both cases were equal.

In the case of the date-seed, Grüss ('96, p. 421) found the resting endosperm to be practically free from enzyme by the guaiac-hydrogen-peroxide test. In the endosperm of germinating seedlings ('96, p. 422) he found by test isolated blue spots indicating the local generation of enzyme independently of the embryo. But concerning this it may be said that as long as the cotyledon was present during germination such a test cannot be regarded as demonstrating independent activity by the endosperm. In summarizing the work of Grüss we may say that the autolysis of the endosperm in the cases of barley and maize is proven only in so far as the guaiac-hydrogen-peroxide test is specified for the presence of hydrolizing enzymes. In the case of the date there is little approach to convincing evidence.

Hansteen ('94, p. 426) regards Van Tieghem's conclusion, concerning self-digestion as occurring in oily seeds but not in amylaceous seeds, as untenable. First, because Van Tieghem made no provision for the escape of the products of digestion. The accumulation of such products in starchy seeds would soon inhibit further digestion. Such inhibition in the case of oily seeds would, however, occur much later, because the oil is first changed to transitory starch and considerable disappearance of oil might be noted before the accumulation of the products of starch transformation would inhibit further digestion. Second, because Hansteen considers himself to have demonstrated that isolated endosperms of barley and corn under sterile conditions of germination favourable to the escape of digestion-products are self-digesting to a considerable extent, and that actual depletion and corrosion of the grains may be noted. The surrounding water into which the digestion-products diffuse becomes reducing to Fehling's

solution. The only objection to Hansteen's tests are, first: that he allowed the grains to soak for two days before removing the embryo, so that the possibility of the diffusion of enzyme from embryo to endosperm is open. That this is a valid objection is recognized by Brown and Escombe ('98, p. 11). On the other hand, Pfeffer ('97, p. 612) regards Hansteen's experiments as demonstrating the capacity of corn and barley endosperms for auto-depletion. Second, he does not show that the endosperm does not already contain some reducing sugar, which, if present, could easily diffuse into the surrounding water.

Linz ('96, p. 311) has shown that in isolated endosperms of maize under conditions of germination a marked increase in sugar content occurs during a period of twelve days. But since he allowed the grains to soak for two days before removing the embryos it is impossible to attribute this increase of sugar exclusively to the activity of enzymes in the endosperm. He draws the unqualified conclusion that the endosperm is living matter. A similar objection may be taken to Linz's ('96, p. 318) unwarranted conclusion that in such endosperms it is not the aleurone layer which furnishes the enzyme. He merely found that after two days' soaking the aleurone layer contains less enzyme that the endosperm, which may mean that during the two days' soaking enough enzyme diffused from the aleurone layer to establish the relative distribution he found. Brown and Escombe found that the aleurone layer (barley) only contains enzyme, and that the corrosion of starch is more notable in the tissue contiguous to it. Moreover, this observation disagrees with that of Grüss ('93, p. 288) who found the aleurone layer and scutellum to contain a much greater quantity of enzyme than the endosperm in the case of seedlings whose hypocotyls had elongated six or seven centimeters.

Leclerc du Sablon ('97, p. 395) made analyses of the date-seed before and after germination. He found oil and sugar to be present in the resting endosperm, together with some little aleurone intermixed with the protoplasm. The sugar is present in only about 1 per cent., and is to be regarded as a saccharose, since it reduces Fehling's solution with precision only after boiling with acid. The carbohydrates insoluble in 90 per cent. alcohol, but soluble in water, are present in only about 2 per cent. Determinations of the amount of sugar present in the resting endosperm were made, and also in the endosperm during germination, when the radicle had elongated to various lengths. His results show a constant increase in the sugar content of the endosperm, but he regards the increase as insignificant, and concludes that the date endosperm is incapable of self-digestion. Examination of his data reveals that he found 0·019 grms. of sugar in a quantity of endosperm tissue when the radicle measured 0·50 cms., and when the radicle measured 4·0 cms. he found 0·024 grms. which is an increase of 26 per cent. Such an increase would be significant

if occurring in the endosperm under conditions which would permit us to say that the embryo had no influence. Sablon notes the interesting fact that during germination the relative quantity of oil in the undigested portion of the endosperm remains about constant, 7 to 9 per cent. He also finds that the sugar and dextrin also remain about constant, but that the resting grain contains a little more because it has not lost by exosmosis. He concludes that the enzyme from the embryo does not penetrate the endosperm.

Puriewitsch ('97, p. 13) studied the depletion of the date endosperm, and concluded that it is capable of auto-digestion. How such a conclusion could be drawn from the data he has recorded cannot be understood. In the first place he allowed the seeds to germinate in sand until the radicle was from 3–7 cms. long. This would require, according to temperature, from two to four weeks, and enzyme from the embryo would certainly pass into the endosperm. Newcombe ('99, p. 68) found an enzyme in the endosperm during later germination, and if my own conclusion is correct, that an enzyme cannot be detected in the resting endosperm, it is evident that such diffusion must occur during germination [1]. Moreover, Puriewitsch does not record actual evidence of digestion. He found merely that the 'culture fluid' was reducing to Fehling's solution. This is not significant, because the resting endosperm contains reducing substance, and further the tannin present would give the same reaction. As a matter of fact his record furnishes more evidence for a negative conclusion, because in microscopic sections of his material he did not find any notable difference between test objects and controls. How could auto-digestion be attributed to a tissue which, after thirty-six days at 27° C., showed no evidence of dissolution as compared with controls? Further he regards the endosperm as living matter capable of initiating and continuing vital processes ('97, p. 16).

In '98, after the researches of Hansteen and Puriewitsch, which are regarded by Pfeffer ('97, p. 613) as demonstrating that the endosperms of barley, maize, and date are capable of self-digestion, Brown and Escombe ('98, pp. 3–24) undertook a reinvestigation of the work of Brown and Morris ('90, p. 458). After quoting the general conclusions of the latter as follows: 'Although the peripheral layer of the endosperm, the so-called aleurone-layer, undoubtedly consists of living cells, no evidence could be obtained of the existence of any residual vitality in the amyliferous cells which constitute by far the greater portion of the endosperm,' they state that there is a general agreement in the work of Hansteen, Pfeffer, Grüss,

[1] Puriewitsch makes a brief statement which shows that this source of error was not overlooked, but he does not show that the error was actually avoided. His statement seems to refer to the cereal endosperms especially, and cannot be applied to the date, because in the text descriptive of manipulation in the date experiments he states that the seeds were allowed to germinate.

and Puriewitsch that the amyliferous cells of the endosperm of the grasses have a definite power of digesting their reserve materials, this power being entirely independent of any influence of the embryo, the only necessary condition for its exhibition being that the products of metabolism shall not be allowed to accumulate within the endosperm.

As a result of this reinvestigation Brown and Escombe ('98, p. 14) have demonstrated a hydrolytic capacity of the aleurone cells of barley. Degermed endosperms steeped in saturated aqueous chloroform twenty-four hours show no depletion for several days, until invaded by organisms, while others not chloroformed show marked sub-aleuronic depletion and dissolution of starch grains. Cytological study of aleurone cells shows a 'well defined nucleus and all the usual cytological evidence of activity,' and these cells are commonly regarded as living units. They also find ('98, p. 18), from a cytological study of the amyliferous cells (barley), that the latter are in a very different condition from that of the aleurone cells. The nucleus is deformed, and the general structure indicates senescence. Actual trial showed the amyliferous cells to be without digestive capacity. Endosperms without embryos or aleurone, under favourable conditions for germination and removal of metabolic products, showed no difference as compared with similar ones treated with saturated aqueous chloroform for twenty-four hours. No visible changes occurred in either case until appearance of organisms, when visible changes did occur, so that it is possible, though rather improbable, that changes might have occurred later if the organisms had been kept out. This work of Brown and Escombe may, then, be regarded as demonstrating the capacity of the aleurone layer of barley for endosperm depletion and as rendering such capacity on the part of the amyliferous cells highly improbable.

The literature thus examined shows that auto-digestion by the amylaceous endosperms of grasses or by the horny endosperms of palms has not been successfully demonstrated, although such a claim has been made by different authors, and this claim has been accepted hitherto. On the other hand, the presence of an enzyme in the aleurone cells of barley has been demonstrated, and Puriewitsch has made reasonably certain a similar statement for other cereals. The question of the vitality of either aleurone cells or of endosperm cells is quite open, for the simple reason that actual vitality tests have not been applied. The work of Brown and Escombe above cited indicates, but does not demonstrate, that the aleurone cells are living, and that the amyliferous cells are not.

INVESTIGATION.

Material and its preparation.—By applying to a large wholesale candy house I was able to secure a large quantity of seeds without buying the fruit. There is a further advantage in that such firms get the best and

freshest, so that seeds saved from such fruit are large and nearly all capable of germination. The seeds so obtained are partially cleaned, but it is always necessary to wash them thoroughly without soaking, after which they may be stored in a dry place for use as needed. The fleshy mesocarp contains reducing sugar.

In all the material used embryo substance was absolutely excluded. This was accomplished by rotating the point of a pocket-knife in the embryo cavity of each and every dry seed until, by examination, all traces of embryo substance were removed. In all the material used this task was done by myself. Since the membranaceous endocarp which still clings to the seeds as so far cleaned contains tannin, it is necessary to remove this in some way. This may be accomplished either by sifting over an air blast after each grinding, and before the powder becomes at all fine, or by washing and drying rapidly after each time through the mill. By either method so little tannin remains that digestion in water at ordinary temperature for six hours gives a liquid which does not react with ferric chloride. Both methods were used: the former before it was known that the contained proteids are insoluble in water, and the latter after.

Estimation of the hydrolytic product.—Having found Fehling's solution unsuitable for my purpose, I decided to find a method which would give me more reliable data. Since starch, dextrine, and enzyme are insoluble in 95 per cent. alcohol, while the reducing sugars arising from enzyme activity are soluble, this reagent was employed for separation. The following test shows the efficiency of such a method. A solution of soluble starch[1] was made, and its content of anhydrous starch per cubic centimeter determined by evaporating over steam triplicate volumes, drying the residue at 110° C. for one hour, cooling in the desiccator and weighing. The anhydrous content of a filtered solution of amylopsin was similarly determined. It was thus possible to titrate a given weight of starch with a given weight of enzyme, and then to determine the weight of the hydrolytic product as follows: After digestion the solutions were made 95 per cent. alcoholic and then allowed to stand until the precipitate settled. The alcoholic solution was decanted, filtered, the precipitate washed with alcohol and the filtrate then evaporated to dryness over steam in tared beakers. The residue was air-dried at 110° C. to constant weight. This residue is brown, with a sweetish, toast-like odour, very hygroscopic, easily soluble in water, and reduces Fehling's solution, but the reaction is not precise, and much of the precipitate remains in suspension for some time, but finally settles. From the following tables it is evident that the hydrolytic product soluble in alcohol is very constant for a given ratio of enzyme to starch.

[1] Dry potato starch was extracted with glycerine (180°–190° C.) for thirty minutes and precipitated with alcohol. Purification was accomplished by reprecipitation with alcohol from aqueous solution.

All the figures represent anhydrous weight in grams. Three ratios of enzyme to starch were tried in duplicate. The starch solution contained in 1 cc. 0·01625. The enzyme solution contained in 1 cc. 0·00160. Titration closer than ·1 cc. not attempted.

	Enzyme.	Starch.	Hydrolytic Product.
1:100	No. 1—0·004960	0·500	0·4700
	No. 2—0·004960	0·500	0·4700
1:200	No. 1—0·002560	0·500	0·4870
	No. 2—0·002560	0·500	0·4950
1:300	No. 1—0·00160	0·500	0·4180
	No. 2—0·00160	0·500	0·4150

These figures show that a reasonably accurate determination of hydrolytic product can be made with varying dilutions of enzyme. Such a determination is far more satisfactory than the usual colour method with iodine. The enzyme used was advertised to convert into dextrine and maltose 250 times its own weight of starch in three hours at about 40° C. The fact that the hydrolytic product for the ratio 1 : 200 is greater than that for the ratio 1 : 100 is to be attributed to difference in digestion conditions, since no attempt at comparison was made except for the duplicates of a given ratio. As dextrine is known to be one of the products of enzyme activity, since dextrine is insoluble in 95 per cent. alcohol, it is evidently excluded in this method. Since the ratio of the hydrolytic product thus obtained is so constant for a given ratio of enzyme to starch, it must be regarded as a very convenient and accurate method for testing the hydrolytic capacity of a given enzyme.

In applying this method to the study of the Date it was found necessary to evaporate to dryness and then extract with alcohol instead of depending upon the alcohol to precipitate all unhydrolized matter. This evaporation must continue until the residue is hard. If to the viscous residue alcohol be added, some of the carbohydrates, though insoluble in alcohol, mix with it and when heated an apparently clear solution is obtained. The alcoholic extract should cool to room temperature before filtering. Failure to observe these precautions gave me results from which a conclusion contrary to the one here given was published[1].

During extraction with alcohol the beakers were covered with watch crystals thus making a sort of reflux condenser.

Properties of the aqueous extract.—The powdered endosperm (400 grms.) prepared as described above yields, after about six hours' digestion with distilled water (1,200 cc.), a liquid which when filtered has the following properties. It is neutral to litmus and remains neutral until by putrefaction it becomes acid. It does not contain tannin, as the test with ferric chloride

[1] Pond, '04, p. 181.

was negative. It does not contain coagulable proteid, for on boiling with acetic acid in several dilutions no flocculation occurred. Care was taken to acidify after boiling and not before. On standing twenty-four hours after boiling there was so sediment. Prompt disappearance of turbidity on acidification suggested the presence of phosphates (tribasic calcium phosphate). On testing with molybdic solution a fine yellow precipitate fell promptly, and on standing twenty-four hours an abundant yellow sediment settled (ammonic-phospho-molybdate). The extract, in contact with concentrated nitric acid, failed to give even the slightest turbidity at junction or anywhere, which suggested the absence of all forms of proteid matter except perhaps secondary proteoses and peptones. The xanthroproteic reaction is doubtful, because the extract has a faintly yellow colour and a slight opalescence. The colour, slight as it is, turns to orange with alkali (NaOH and NH_4OH), and similar change occurs with concentrated nitric acid, the colour in the latter case deepening on addition of alkali. Reversing the order of addition reverses the effects, or if heat is generated other colours, such as brown or reddish-brown, are produced. The colouring matter does not react sharply however. The same tests with commercial tannin did not give identical results, although various colourations were obtained. Dilute alkali causes the change of colour but dilute acid does not. The opalescence is, however, destroyed by both reagents. Glacial acetic acid does not produce visible change. Mineral acids, however, if concentrated, seem to have decided positive effect.

Negative results were obtained in the following tests for proteids: Mayer's reagent, Millon's reagent, acetic acid and potassium ferrocyanide, and boiling in an acidified, saturated solution of ammonium sulphate. The latter solution, after filtering, was negative in the Biuret test. The latter reaction and the xanthroproteic test are not reliable with the extract because the colour produced by the alkali or strong acid obscures any evidence of change.

The extract reduces Fehling's solution if not too much reagent is used. If some freshly prepared reagent is diluted and boiled, and then the extract be added slowly, a prompt reduction occurs very soon. If the reagent is present in excess the reduction may not occur. In some cases I noted a heavy flocculation without reduction. This flocculation was found to be produced by the copper sulphate alone. On removing the precipitate the filtrate was promptly reducing. That this reduction was not due to tannin is certain because the test with ferric chloride was negative.

The reaction with phenylhydrazin is positive. Carbohydrates insoluble in alcohol are present, and they may be fractionally precipitated with different strengths of alcohol, but very little precipitation occurs after a concentration of 80 per cent. is reached. The substance precipitated by alcohol when dried is of a dirty white colour and partially soluble

in water. It does not respond to any of the tests for proteids. This behaviour excludes albumins and globulins, and adds emphasis to the negative tests with the extract itself. These observations do not agree with those of Puriewitsch ('97, p. 66) who obtained flocculation on boiling his 'culture fluid' with acetic acid, and a white precipitate with acetic acid and potassium ferrocyanide. Either his observations were faulty or else some coagulable proteid passed from the embryo to the endosperm during germination.

Extraction with sodium chloride. The same powder, after the preceding extraction with water, was digested with 5 per cent. sodium chloride for sixty hours (toluol, 5 per cent.). This extract was neutral to litmus. On heating, a milky turbidity appeared which was more opaque than was that of the aqueous extract. The heating was continued to boiling for a minute, when a flocculent precipitate appeared which redissolved on cooling and reappeared on heating. The turbidity was destroyed by acetic acid and did not reappear until the acidity was neutralized by ammonium hydroxide. Other reactions agreed with those of the aqueous extract, except that a white precipitate formed with acetic acid and potassium ferrocyanide. This latter result was found to be due to impurities in the toluol, as the acetic acid alone with the toluol gave the white precipitate. The flocculation on boiling was found to be due to impurities in the sodium chloride. This leaves the sodium chloride extract negative in all tests for proteids, just as was the aqueous extract, and positive for phosphates. The sodium chloride itself did not react for phosphates with molybdic solution.

Extraction with sodium hydroxide, ·1 per cent. The residue remaining after the extraction with sodium chloride was digested sixty hours with sodium hydroxide, ·1 per cent. and toluol, 5 per cent. The filtered extract was found to be only slightly alkaline so that the alkalinity had evidently decreased during the digestion. This extract does not have the opalescent hue of the other extracts but instead is of a deep amber colour. This colour is undoubtedly due to the alkali, as it appeared almost instantly when the latter was added. As the neutral point was slowly approached with acetic acid the amber gradually disappeared, being replaced slowly by a dirty opalescence. As the reaction became faintly acid a cloud was noticed, which gradually spread through the liquid as the reaction became distinctly acid. On standing a few minutes this turbidity developed to a flocculation and a curdy precipitate finally settled.

This precipitate changed to brick red on boiling with Millon's reagent. The filtrate did not react with any reagents for proteids nor with ammonium sulphate. The extract itself did not respond to any of the proteid tests except with ammonium sulphate. The latter test was positive because the small amount of proteid present was concentrated into a precipitate. Coagulation did not occur when the extract was boiled at the neutral point.

Another extract was made from fresh dry powder. After two hours digestion the brownish red extract gave a precipitate at the neutral point. Continuing the extraction over night (sixteen hours), the extract did not give a precipitate at the neutral point, and boiling at the neutral point was without apparent effect. When slightly but distinctly acid the precipitate settled.

Extraction with sodium hydroxide, 2 per cent. The residue remaining after the extraction with sodium hydroxide, ·1 per cent., was exhausted sixty hours with a 2 per cent. solution of the same reagent. The powder immediately turned a dark blood red with a brownish tinge. The filtered extract was of course alkaline. On close neutralization with acetic acid no change occurred, not even after boiling. Continuing the acidification slowly, no change was apparent when a decided acid reaction was attained, but continuing still farther the brownish tinge gradually disappeared, and when strongly acid a change to cherry red occurred, and a copious flocculent precipitate settled. This result made it clear that a fairly large amount of proteid can be extracted with a proper strength of alkali. The ·1 per cent. alkali is evidently too weak to extract all the proteid. Since the 2 per cent. alkali, however, might have effected some decomposition of the proteid, it seemed best to try a moderate strength.

Extraction with sodium hydroxide, ·5 per cent. On adding 500 cc. of ·5 per cent. NaOH solution to 500 grms. of freshly prepared powder the usual change to brownish red occurred. After forty-eight hours it was noticed that this colour had disappeared, and the reaction was found to be acid to litmus[1]. The same volume of alkali solution was then added and the brownish red colour returned and remained for sixty hours. On acidification with acetic acid the filtered extract yielded a copious flocculent precipitate. The latter, after fusing with caustic potash, gave an unusually abundant yellow precipitate of ammonic-phospho-molybdate. This result, in connexion with the data already recorded, may be accepted as evidence of the presence of considerable nucleoproteid. The wet precipitate resembles the extract in colour, being perhaps more brown than red. No colour was imparted to any of the following reagents on stirring the still wet precipitate into them: aceton, methyl alcohol, ethyl alcohol, benzol, petroleum ether, turpentine and carbon bisulphide. Some of the matter which colours the precipitate is soluble in hot water, and this solution gave a weak reaction for tannin with ferric chloride[2].

Why this extract became acid after forty-eight hours while the ·1 per cent. extract was still alkaline after sixty hours is not known. The two cases are not comparable, however, because one was with fresh powder and the other with material which had been successively exhausted with water and sodium chloride.

[2] The remainder of the precipitate was studied further by Dr. Gies, as far as the quantity would permit, and the following observations were made by him. After drying at room temperature and being reduced to a powder, which was dark red, the precipitate was redissolved in dilute alkali

Demonstration of tannin in the endocarp. The thin membranous endocarp may be obtained in quantity as a chaff by sifting the powder, especially after the first time through the mill. On boiling some of this endocarp chaff in water, a light brown solution was obtained, which gave with ferric chloride a brown precipitate and a brownish green filtrate. By using a more dilute solution of the reagent a typical blue green colour without a precipitate was obtained, On adding lead acetate a grey precipitate fell leaving a water clear filtrate. Potassium ferrocyanide caused a grey precipitate to fall. Iodine gave a reddish brown precipitate.

A cold aqueous extract of the endocarp chaff gave a typical reduction of Fehling's solution, probably due to the reducing sugar held by the membranes. Another portion of chaff, after being washed until an hour's aqueous extract at ordinary temperature did not reduce Fehling's solution, was extracted with boiling water. This extract reduced Fehling's solution, presumably because of the tannin rather than because of sugar. That tannin was present was made certain by the test with ferric chloride. Further, this extract gave the same colour reaction with alkali as the powdered endosperm from which the tannin was not obtained after long digestion in cold water. The endosperm substance entirely freed from endocarp substance by scraping the dry seed does not develop this colour with alkali. Thus it seems probable that the endosperm powder prepared as previously described above contains so little tannin or associated substances that not enough goes into solution in cold water to react with ferric chloride, but that enough is present to produce the change noted when alkali is added.

Recapitulation of preceding data. The facts of special interest now revealed are: the endosperm contains reducing sugar, the endocarp contains tannin, the only proteid present in significant amount is the nucleoproteid.

Experiment No. 1. Is the aqueous extract of the resting endosperm auto-hydrolytic? For this test 400 grms. of powdered endosperm were

(KOH, 2 per cent.) and reprecipitated by slight acidification with dilute acetic acid. This process was conducted three times. The filtrates were amber coloured. The final precipitate seemed as deeply coloured as the first. The filtrates were free from phosphate. The precipitate contained phosphorus. On digestion in pepsin-hydrochloric-acid (2 per cent. each), a slight residue resembling the original precipitate remained, containing phosphorus. It was soluble in dilute alkali and appeared to be a nuclein or a mixture containing it. Hydrated with 2 per cent. HCL a deep red solution was formed, and a brownish black, flocculent material collected. The latter was slowly soluble in dilute alkali and, after being reprecipitated with acid, the colour remained the same and no effort was made to determine the nature of the latter. The filtrate was made strongly alkaline with NH_4OH. Treatment with an excess of ammoniacal silver solution had no effect. There was no precipitate of silver-purin compounds after standing twenty-four hours. These observations indicate that the original precipitate is not a pure substance. It contains not only nucleoproteid but apparently the colouring matter already noted. It is possible also that other substances or compounds of nucleoproteids are present, and further study with more material would be necessary to establish definite conclusions.

used. This quantity of powder was digested fifteen hours in the refrigerator (12° C.) in 1500 cc. of tap-water which had been filtered through a Berkefeld filter. No antiseptics were used, the low temperature sufficing to inhibit putrefaction, as was shown by the neutral reaction of the filtered extract. The test for tannin in the filtered extract was negative, so 75 cc. of it were delivered from pipette into each of four beakers. Two of these beakers, group 1, were immediately evaporated to dryness over steam. The remaining pair, group 2, were digested eight days at 35° C. During this period a strength of 5 per cent. toluol was maintained. The beakers were covered with a watch crystal and stirred daily. After evaporating to dryness the duplicates of group 2, all four beakers were then extracted with 95 per cent. alcohol by boiling for three hours. After cooling and decanting over night, the alcoholic extracts were filtered into four tared beakers and evaporated to dryness over steam. The residues thus obtained were dried to constant weight at 120° C. and being very hygroscopic were cooled in the desiccator and weighed as rapidly as possible. The duplicates of group 1 were respectively ·5765 grm. and ·5805 grm., while those of group 2 were ·5465 grm. and ·5610 grm. Evidently the quantity of monoses in solution did not increase and hydrolysis could not have occurred. Since the aqueous extract contains non-reducing carbohydrates, which are converted into reducing sugars by the action of dilute acids, no reason is apparent why hydrolysis should not have taken place, if any enzyme were present, unless it might be that the non-reducing carbohydrates were present in sufficient amount to inhibit any enzyme action. That this was not the cause of the negative result seems clear from the results of subsequent experiments. That the temperature of digestion was favourable must be assumed because the seed germinates much more rapidly at this temperature than at lower ones.

Experiment No. 2. Is the endosperm powder capable of auto-digestion? Into each of four beakers 25 grms. of powdered endosperm were placed. The weighing itself was accurate, but no attempt to get the actual weight of the powder was made, the moisture remaining after three days' exposure to room temperature after grinding being included. Into each of two of these beakers 75 cc. of 1 per cent. $CuSO_4$ were delivered from pipette, and into each of the remaining two were placed 75 cc. of 1 per cent toluol. All four beakers were incubated ten days at 35° C., being stirred daily and the toluol renewed. On the tenth day the liquor from each beaker was filtered, and into four tared beakers 50 cc. of each filtrate were respectively placed. The anhydrous alcohol soluble residues were: toluol, ·4326 grm. and ·4110 grm.; copper sulphate, ·4400 grm. and ·4647 grm. The latter residues were coloured by the copper sulphate and no doubt a small amount of the latter was

dissolved by the alcohol, but this would not affect more than the second decimal place. The figures certainly indicate a negative result, and the only possible objection is that mentioned in the preceding experiment, namely, the inhibition of enzyme activity by the presence of substances in solution.

Experiment No. 3. Does an enzyme develop in the endosperm during germination? In experiment number 1, the aqueous extract was from the resting endosperm. In experiment number 2, the endosperm substance was under conditions comparable to those of germination, except that aerobic respiration was impossible and the escape of any hydrolytic products could not proceed normally. So it seemed best to test the behaviour of endosperms which had been under conditions favourable for germination. For this purpose a quantity of degermed but otherwise whole endosperms was divided into two groups. The individuals of group 1 were located on a perforated, floating board so that each rested in a thin film of water. The volume of water which floated the board was about twenty litres and this was renewed daily. The endosperms were kept sterile by washing them for three minutes daily in a one per cent. solution of copper sulphate. The germination of a few seeds whose embryos were intentionally left undisturbed was not prevented by this treatment. That is, of course, the radicles protruded. The individuals of group 2, intended as controls, were placed in crystallizing dishes and enough one per cent. copper sulphate solution added to about one half submerge them. This solution was renewed every three days, so as to make the loss by diffusion comparable with that occurring in group 1. After twenty-eight days at room temperature, the endosperms were ground and the tannin removed as usual. With the powder thus obtained a repetition of experiment number 2 was made, except that the residue from 25 cc. of filtrate was determined instead of from 50 cc. The residues of group 1 were ·1310 and ·1360 grm. Those from group 2 were ·1835 and ·1883 grm. Evidently there is no more manifestation of enzyme in this experiment than in the preceding ones. The possibility of the same disturbing factor was not excluded, however, although its potency would necessarily be reduced by the loss of substance from the endosperm during the period under conditions of germination.

The residues are less than one half those found in the preceding experiment. This would be expected, as sugar originally present was lost by diffusion during the twenty-eight days under germination conditions. In both cases the copper sulphate residues are larger, and since by calculation from the solubility of copper sulphate in alcohol, it may easily be seen that not all of the difference can be attributed to this, it seems quite probable that the escape of sugar from the endosperm

proceeds more slowly in the copper sulphate solution. This granted, the result is just what would be expected as a consequence of simple exomose in the absence of enzyme.

Experiment No. 4. Do degermed but otherwise whole endosperms show any internal corrosion or evidence of auto-digestion after a long period under optimum conditions of germination? While preceding tests render a negative answer highly probable, the following experiment was made as a conclusive test. Twenty degermed and carefully cleaned endosperms were placed in a vertical position behind a rubber band which encircled a small crystallizing dish. The preparation was then placed in a dish containing sufficient 1 per cent. toluol to leave the endosperms standing about one-fourth submerged. Diffusion and escape of hydrolytic products were thus well provided for and respiration was not interfered with. The preparation was then kept in the incubator at 35° C. for fifty-six days. A control preparation in 1 per cent. copper sulphate was carried. The solutions of these preparations were, with few exceptions renewed daily. The toluol of this strength is such a weak antiseptic that a daily renewal is necessary as also the bathing of the unsubmerged portions of the endosperms. Seeds will commence germination under these conditions.

At the conclusion of the test period the endosperms were sectioned, stained in Bismarck brown and mounted in glycerine. After clearing over night microscopic examination failed to reveal the slightest evidence of auto-digestion. The walls were intact. No such corrosion markings as figured by Grüss ('94 a, taf. 14 and 15) could be found. Comparison was made with dry resting endosperms but no positive difference could be detected. The middle lamella showed very plainly in all three sets of sections, but no difference either in cell wall or cell contents could be noted.

Conclusion:—The endosperm of *Phoenix dactylifera* is incapable of self-digestion.

While this investigation has been continued intermittently for some years, the major part of the results here recorded have been obtained during my incumbency of a research scholarship, June, July, and August, 1905, in the New York Botanical Garden. I am especially indebted to Professor Wm. J. Gies, consulting chemist of the Garden, and to Dr. D. T. MacDougal, assistant director, for advice and facilities in carrying out the work.

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The Influence of Correlation upon the Size of Leaves.

BY

ALFRED J. EWART, D.Sc., PH.D., F.L.S.

With two Figures in the Text.

ACCORDING to Lindemuth[1], leaves of *Begonia rex* and of *Iresine Lindeni* which have been allowed to root in soil increase in size, and this increase is due not to any multiplication of cells but to an enlargement of the individual cells. It remains an open question whether the enlargement is directly due to a rise of turgor in the extensible cells of the leaf, or whether it is a true growth reaction awakened by some correlative influence. In any case it seemed of interest to determine whether a similar expansive enlargement can be produced on the leaves of an ordinary tree after they have ceased to grow, and a lime tree (*Tilia europaea*) was selected for the experiment.

On April 1, all the buds were removed from a branch 145 cms. long and 2 cms. diameter at the base, excepting the terminal one, and new buds were removed as fast as they developed. The branch produced 3½ times as many buds as would normally develop. Measurements in centimetres of the leaves were taken on June 27, the length and breadth of the lamina being those of an inscribing rectangle traced on paper (Fig. 1). At the same time an average was taken of the larger leaves on normal shoots, and also of the smallest first formed ones.

	Petiole.	Lamina. Breadth.	Lamina. Length.	Internode.
Defoliated Branch.				
1st leaf	3	6·2	7	
2nd leaf	4·5	7·8	8·1	0·5
3rd leaf	5·2	11·5	14·2	1·5
4th leaf	5·0	11·2	15	3·2
5th leaf	4·2	12·5	17·1	4·7
6th leaf	3·5	13·2	16·2	8·1
7th leaf	2·5	13·2	16·8	8·6
Normal Branches.				
Average of largest adult leaves	4·4	7·7	10·1	4·5[2]
Average of smallest adult leaves	1·5	3·0	3·2	2·8[3]

[1] Ber. d. D. Bot. Ges., xxii, 1904, p. 171.

[2] Average on largest normal shoots.

[3] Average on smallest normal shoots.

All the leaves were now removed from the defoliated shoot except 1 and 2, which on August 30 measured:—

		Lamina.	
	Petiole.	Breadth.	Length.
1st leaf	3	6·3	7·1
2nd leaf	4·5	7·8	8·2

No increase in size had therefore occurred, since a difference of a millimetre is about the limit of error in measuring the lamina by this method, and the shape of the leaf precludes accurate direct measurement. Nevertheless, the removal of the lower buds in spring caused the remaining one to develop abnormally large leaves, as is well shown by the photograph reproduced in Fig. 2.

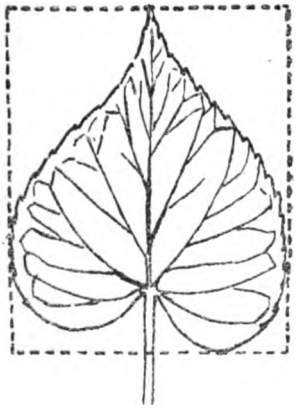

FIG. 1. Mode of measurement of leaf.

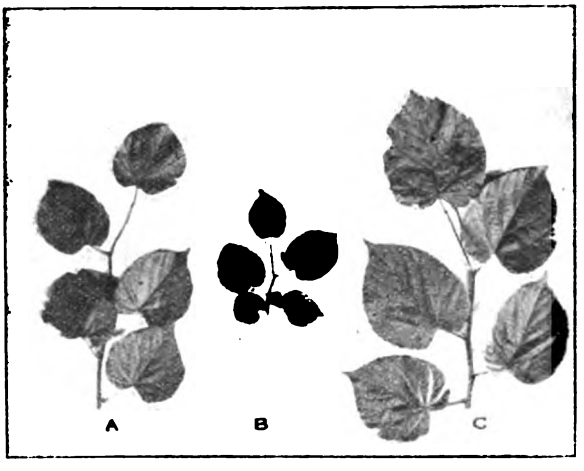

FIG. 2. A. Largest normal terminal shoot and leaves. B. Smallest ditto. C. Terminal shoot and leaves on defoliated branch. All from the same plant of *Tilia europaea*.

On June 10, two branches were selected 250 cms. long and 3 cms. thick at the base, and all the leaves and buds were removed except in the terminal shoot of each, whose leaves had ceased to grow. All new buds were continually removed, but the number was relatively few. The following figures give the measurements of the first branch on June 10, the numbers in brackets being the measurements on August 30:—

		Lamina.		
	Petiole.	Breadth.	Length.	Internodes.
1st leaf	1·9 (1·9)	4·7 (5·0)	5·6 (5·5)	1·0 (1·0)
2nd leaf	2·9 (3·0)	6·4 (6·5)	7·0 (7·1)	1·9 (1·9)
3rd leaf	3·5 (3·5)	8·0 (8·0)	8·8 (8·8)	3·9 (3·8)
4th leaf	2·8 (3·0)	7·4 (7·5)	9·5 (9·5)	3·2 (3·3)
5th leaf	3·0 (3·0)	6·0 (6·1)	7·7 (7·8)	3·5 (3·5)
6th leaf	2·0 (2·0)	5·7 (6·1)	7·2 (7·3)	

Apart from an apparent very slight increase in breadth which might easily be due to a greater divergence of the leaf teeth, or to a flattening of the lamina, no increase in size is shown.

The second branch had an erect glass tube filled with water attached to a side branch near to the apex, and on this branch and ultimately on a neighbouring one, a new surface was cut every second day for the entry of water. It was not found possible to maintain a greater pressure than 10 ft. of water, since beyond this pressure the water passed backwards rapidly into the main trunk. A pressure of from 6 to 10 ft. was, however, maintained for a month, and the measurements in brackets were taken on August 30:—

		Lamina.		
	Petiole.	Breadth.	Length.	Internode.
1st leaf	2·3 (2·4)	6·6 (6·6)	7·5 (7·4)[1]	0·7 (0·8)
2nd leaf	2·9 (2·9)	7·0 (7·0)	8·2 (8·2)	1·5 (1·5)
3rd leaf	3·3 (3·5)	8·5 (8·8)	10·0 (9·8)[1]	3·4 (3·4)
4th leaf	3·3 (3·5)	8·5 (8·6)	11·2 (11·2)	3·7 (3·7)
5th leaf	3·0 (3·1)	7·8 (8·0)	10·1 (10·4)	

Hence, neither the effect of an unusually abundant supply of water nor of the correlative influences due to the removal of the other buds and leaves are able to excite any renewed growth in an adult leaf of *Tilia*, even when acting conjointly. These influences, possibly aided by a more abundant supply of food, do, however, cause leaves to develop to an abnormally large size when applied at a sufficiently early period of their growth. The increased size is, however, not due to an increase in the size of the individual cells, but to an increase in their numbers.

Thus in sections of a leaf measuring 13·2 × 16·8 and of one measuring 6·1 × 7·4 taken parallel to the midrib, the number of epidermal cells between the ends of a micrometer under the high power at various points was in both cases from 8 to 12, and of palisade parenchyma cells from 20 to 35. Similarly, the following numbers give the maximal divergences in the number of cells across the diameter of the high power field in transverse sections at various points of large and small leaves:—

Size of leaf	17·1 × 12·5	3·5 × 3
Upper epidermis	10 to 16	10 to 15
Palisade parenchyma	35 to 52	38 to 48
Lower epidermis	11 to 18	12 to 17

At corresponding points on the two leaves the numbers agreed very closely.

The facts first mentioned hardly agree with the usually accepted idea that the total number of leaf-cells is determined at an early date, and that

[1] Tip slightly withered.

the subsequent expansion of the leaf merely involves an increase in their size, for the large dimensions shown by the leaves on the shoot defoliated in spring were attained owing to a longer continuance of growth, and to a larger production of cells during expansion. The absence of any power of response in the adult summer leaves is possibly correlated with the fact that the power of regenerative bud-development is much less pronounced in summer than it is in spring.

The Development of Fossombronia longiseta, Aust.

BY

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With Plates V and VI, and eight Figures in the Text.

FOSSOMBRONIA longiseta occurs in great abundance in the immediate neighbourhood of Stanford University, as well as in other parts of the state. All material used in the preparation of this paper was collected by the writer within or near the university campus. The work was taken up at the suggestion of Dr. D. H. Campbell, whose valuable advice and guidance is much appreciated. I am also indebted to Dr. Geo. J. Peirce for a number of helpful suggestions pertaining to certain physiological problems in their bearing upon Liverworts, and to Dr. A. A. Lawson for instruction and advice relative to methods, microtechnique and points of cytological interest.

With the exception of the classical work of Leitgeb[1] no comprehensive study of any member of the genus *Fossombronia* has yet appeared. Occupying as it does a position between the purely thallose Jungermanniaceae such as *Aneura* and *Metzgeria* and the higher foliose types, it was thought that a careful study of the species *F. longiseta* might disclose some interesting morphological relationships.

Habitat and External Characters.

Our species of *Fossombronia* appears to be a very adaptive one as to habitat, for while the most thrifty and largest plants are found along moist and well-shaded north-east banks or hill-sides, it is not infrequently found associated with *Sphaerocarpus cristatus* and *Anthoceros Pearsoni*, growing on soil exposed to the sun to a greater or less degree during the day. It occurs in great abundance under the somewhat open growth of the university arboretum, and this habitat seems greatly to enhance the development of antheridia and archegonia at the expense of the vegetative growth. Howe[2] reports it as producing stems 6 to 15 mm. long, and sometimes once dichotomous, but we have occasionally found it under

[1] Leitgeb, vol. iii, pp. 105–20.

[2] Howe ('99), p. 81.

especially favourable conditions attaining a length of 30 mm., and as many as three times dichotomous within one growing season. Fig. 1, Plate V, represents such a plant. A similar extra growth of the thallus has been reported by Campbell[1] for *Sphaerocarpus* under like conditions of light and moisture. *Fossombronia longiseta* is a monoecious species, though it is described by Howe[2] as sometimes developing antheridia to the exclusion of archegonia and vice versa. Further on in his description, however, he states that it is quite probable that, in cases where the plants are perennial, archegonia occur each alternate year. The writer's observations extend over two consecutive years, and verify Howe's statement, though even here there is considerable variation. Plants growing under most favourable conditions of light and moisture quite regularly bear archegonia and antheridia on the same plant in one season, while those growing in the arboretum or in soil exposed to sunlight almost invariably produce the sex-organs separately in alternate seasons.

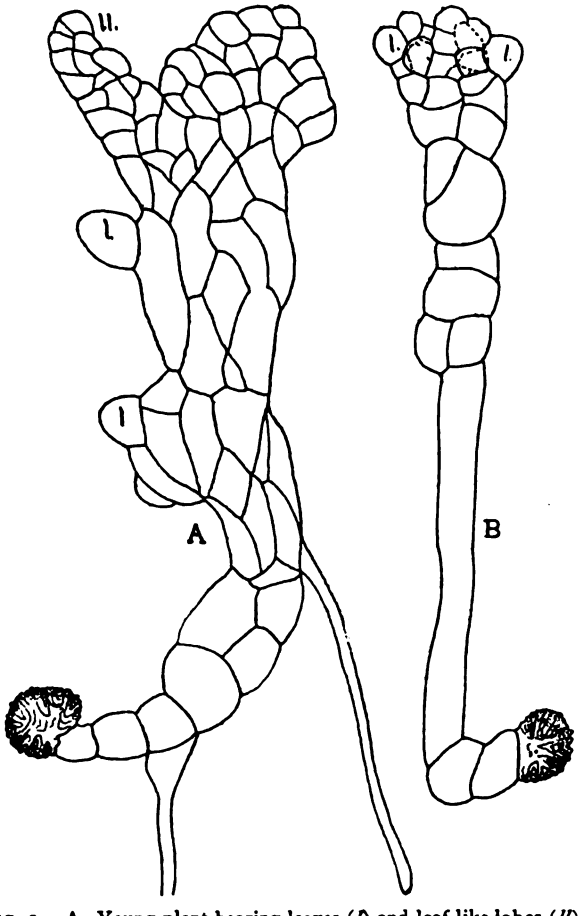

FIG. 1. A. Young plant bearing leaves (*l*) and leaf-like lobes (*ll*). B. A younger plant beginning to produce leaves.

Among the Anacrogynae *Fossombronia* is peculiar in that it represents something of a departure from such thallose forms as *Aneura* or *Metzgeria*, owing to the development of genuine leaves. These are disposed laterally, usually in two rows along the stem, appearing at first as mere outgrowths not greatly differing in appearance from the general structure of the young stem. But as they develop, the leaf-like character is unmistakable. In Text-Fig. 1, A and B represent different

[1] Campbell ('96), Fig. 9.

[2] loc. cit., p. 81.

stages of leaf-growth in very young plants. Normally the leaves range from 1 to $3\frac{1}{2}$ or 4 mm. in length, though it is not unusual to find strong, vigorous plants bearing leaves 5 or more mm. in length.

The leaves are always more or less imbricate and irregularly lobed, the apex of each lobe terminating in a relatively small, somewhat elongated mucilage-cell. These cells are further characterized by the total absence of chlorophyll, and by the presence of a few oil-bodies. Hanstein's Aniline mixture was used as a mucilage test, in each case giving the characteristic mucilage reaction—a marked scarlet red. Iodine was also employed, producing a bright yellow in the older cells, and a deeper brownish colour in the young cells. These mucilage-cells are of the same physiological

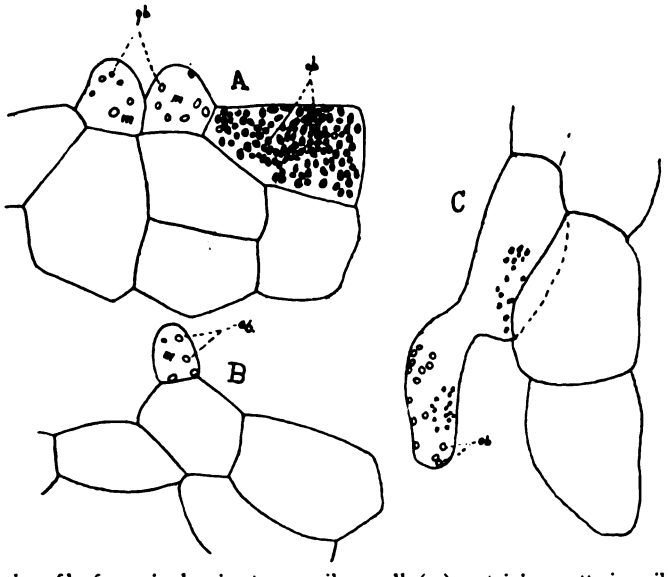

FIG. 2. A. Portion of leaf-margin showing two mucilage-cells (*m*) containing scattering oil-bodies (*ob.*). ×560. B. A similar cell attached to an elevated leaf-cell. ×560. C. A glandula hair. ×560.

significance as the mucilage-hairs that develop upon the surface of the stem, and along with these are of undoubted value to the plant in aiding it to resist the effect of prolonged drought. Early in the autumn of 1903, before the advent of the rainy season, a quantity of the material in a thoroughly dry condition was brought into the laboratory, and a portion of it was moistened. In the course of twenty-four hours the apical ends of the more vigorous plants had revived, and were green to a length of a millimetre or more. Such a sudden revival of so much of each plant suggested the idea that one might possibly find antheridia and archegonia already fairly well developed at the inception of the dry season. Considerable material was examined shortly after being revived, and in many cases nearly mature organs were found that could only have developed before the plants were dried.

In preparing plants for the fixing solution it was noticed that in some cases the stem was more or less thickened, taking on something in the nature of a tuberous growth as shown in Text-Fig. 3. A more detailed examination of the contents of this stem-enlargement revealed the presence of fungal hyphae, and in every case these were always present. In fact, on close scrutiny, it is found that few plants escape infection. Just what is the true relation between the host and the fungus cannot be said, but in a later paper an attempt will be made to throw some light on the problem.

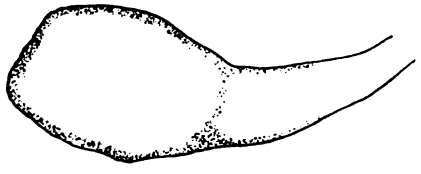

FIG. 3. An example of tubercular thickening of stem. × 112.

It is barely possible that the tuberous thickening of *F. longiseta*, at least as it occurs here, is a pathological structure, functioning physiologically, however, as a storage organ.

No amount of desiccation seems in any way materially to affect the ability of *Fossombronia* to revive, or to influence its rate of growth. Material brought into the laboratory during the dry season was subjected for several days to the action of a powerful drying reagent, in this case glacial phosphoric acid. The material was collected in the latter part of September, from an exposed and thoroughly dry roadside embankment. In the air-dry condition the plants weighed ·107 gr.; after treatment with glacial phosphoric acid till no further loss of weight was perceptible, they were observed to weigh ·102 gr., or ·005 gr. had been given up by the material, or 4·6 per cent. of its air-dry weight represents the actual water-content of the plants before subjection to the drying reagent. Upon removal from the bottle containing the glacial phosphoric acid, they were at once placed in a Petri dish upon damp earth and covered. After twenty-four to forty hours the plants were as green, and as far advanced as those not artificially dried, and within twelve days many spores had germinated that had clung to the material during the experiment. This test has not been applied to the other Archegoniates common to this region of long dry summers, but as stated by Campbell [1] they no doubt possess a degree of adaptation quite as pronounced as that seen in *Fossombronia*.

Experiments by Peirce [2] upon the behaviour of Lichens in this region go to show that the influence of our summer morning fogs is considerable, and it is not improbable that the Hepaticae are more or less affected, to such an extent, in fact, as to cause a slight growth.

The development of tubers or tuber-like thickening of the stem among Liverworts is not uncommon. Goebel [3] has described and figured a species

[1] Campbell ('04), p. 86. [2] Peirce ('99). [3] Goebel ('98), Teil ii, Heft 1.

of *Fossombronia* (*F. tuberosa*), in which well-defined tubers commonly occur. This character is also shared by *Geothallus tuberosus*, Campb., *Anthoceros dichotomus*, Raddi, *Riccia cancellata*, Taylor fide Stephani, *Riccia perennis*, Stephani, *Riccia bulbifera*, Stephani, *Anthoceros tuberosus*, Taylor, *Anthoceros phymatodes*, M. A. Howe, *Petalophyllum Preissii*, Gottsche, *Petalophyllum lamellatum*, Hooker. Howe[1] was the first to call attention to the occurrence of this fact in regard to *Fossombronia longiseta*, stating it to be especially true in specimens from Southern California. Whether the stem-thickening of plants grown in the extreme southern portion of the state is of the same character as that of plants farther north has not yet been determined, and whether the thickening is due to the disturbances set up by the fungus can be definitely ascertained only by cultures on sterilized soil. The fungus seems to be confined almost wholly to the stem and rhizoids, the latter sometimes undergoing modifications in the form of lateral swellings, some of which are strongly suggestive of short branches. In no instance have the sex-organs or sporogonium shown any evidence of infection such as is reported by Leitgeb[2] as occurring in the young sporogonium of *Ptilidium ciliare*; by Garber[3] in *Ricciocarpus natans*; and by Cavers[4] in *Lophocolea bidentata*, *Cephalozia bicuspidata*, *Plagiochila asplenioides* and *Radula complanata*, and in the capsules of *Pallavicinia Lyellii* and *Pallavicinia hibernica*.

Golenkin[5] ('02), described endotrophic mycorhiza existing in *Marchantia palmata*, *M. paleacea*, *Preissia commutata*, *Targionia hypophylla*, *Plagiochasma elongatum* and *Fegatella conica*. According to this writer the fungal hyphae are confined entirely to the compact ventral tissue, and the infected cells never show the presence of starch or chlorophyll, though they still retain their nuclei and protoplasm. In *Fossombronia longiseta* infected cells may contain chlorophyll, and in some cells starch occurs, but in those cells that have reached an advanced stage of infection, neither starch nor chlorophyll could be made out.

The occurrence of fungal hyphae in the rhizoids has been described by Janse[6] for *Zoöpsis* and by Nemeč[7] for *Lophozia bicrenata*, *Lepidozia reptans* and *Kantia trichomanis*. To these species Cavers[8] has added *Cephalozia bicuspidata*, *Scapania nemorosa*, *Diplophyllum albicans*, *Plagiochila asplenioides*, *Bazzania trilobata* and *Porella platyphylla*.

METHODS.

All material was fixed either in the field, where it was at once placed in the fixing fluid, or brought into the laboratory in large sods where it was placed under a bell-jar until time of fixation. Flemming's weak solution

[1] Howe ('99), p. 80. [2] Leitgeb, Heft 2, Taf. iii, Fig. 26. [3] Garber ('04), Pl. X, Fig. 40.
[4] Cavers ('08), p. 30. [5] Golenkin ('02), Bd. xc, p. 209. [6] Janse ('97), vol. xiv.
[7] Nemeč ('99), Bd. vii, p. 311. [8] loc. cit. ('08), p. 35.

gave most satisfactory results, though chrom-acetic and 1 per cent. chromic gave results quite as satisfactory in certain cases. Owing to the delicacy of the plants, thorough penetration of the fixing solution was obtained with no difficulty except in the case of the developing spores. Ordinarily, the material was left in the fixing fluid from six to twenty hours, whereupon it was washed in running water from four to seven hours, and then slowly dehydrated through a series of graded alcohols. Schleicher and Schull's diffusion shells were tried, but allowed of too rapid dehydration and a consequent shrinkage. It was found necessary to change the absolute alcohol at least twice. From the absolute alcohol the material was placed in a solution consisting of equal parts of absolute alcohol and bergamot oil. Turpentine was also tried, but seemed to render the material too brittle to section well, and was consequently dropped in favour of bergamot oil. It was found best by experiment to add bergamot oil to the alcohol gradually, and to transfer to pure bergamot after the lapse of about two hours. Material left in pure bergamot longer than two or three hours was in many cases too brittle. The receptacle containing the pure bergamot oil and the material was then placed in the paraffin bath and heated to about 45° C. To this small bits of paraffin were gradually added until a mixture of about equal parts resulted. The material was next transferred to pure paraffin at a temperature of about 55° C., after having been in the paraffin-bergamot solution from six to eighteen hours, depending upon the nature of the material. It was usually allowed to remain in the pure paraffin about twenty-four hours, and then blocked in small paper boxes and cooled in 95 per cent. alcohol which improves the grain of the paraffin for the knife. Albumen was employed throughout as a fixative. In most cases the sections were treated with the triple stain—anilin-safranin, gentian, and orange G., which gave good results throughout. In certain cases, however, as in spermatogenesis and sporogenesis material, iron haematoxylin and erythrosin or safranin as contrast stains were used with very satisfactory results. Free spermatozoids were fixed upon the slide with osmic vapour and stained with gentian violet. They were afterwards mounted in Canada balsam. The markings on the mature spores were most clearly brought into relief by placing the spores in a solution of 10 per cent. glycerine for a few days, which seemed to clear the exospore, rendering it a light brown.

Germination of Spores.

In September, 1903, a number of capsules, already ruptured, were brought into the laboratory, and from spores clinging to these a number of cultures in different media were started. On September 14, spores were sown in distilled water and in a normal culture solution. On September 26, twelve days later, a few spores were germinating in the distilled water,

and in the course of five days the more advanced ones had reached a stage as seen in Fig. 4, B. Others of the same culture had undergone a nearly vertical division of the young germ-tube. The spores sown in the normal culture solution did not germinate, owing to the action of Bacteria.

On October 12 another set of cultures was prepared in which the above experiments were repeated, and in addition spores were sown in ordinary boiled tap-water and on sterilized soil. This time several spores, after a lapse of twelve days, had germinated in the normal culture-solution while

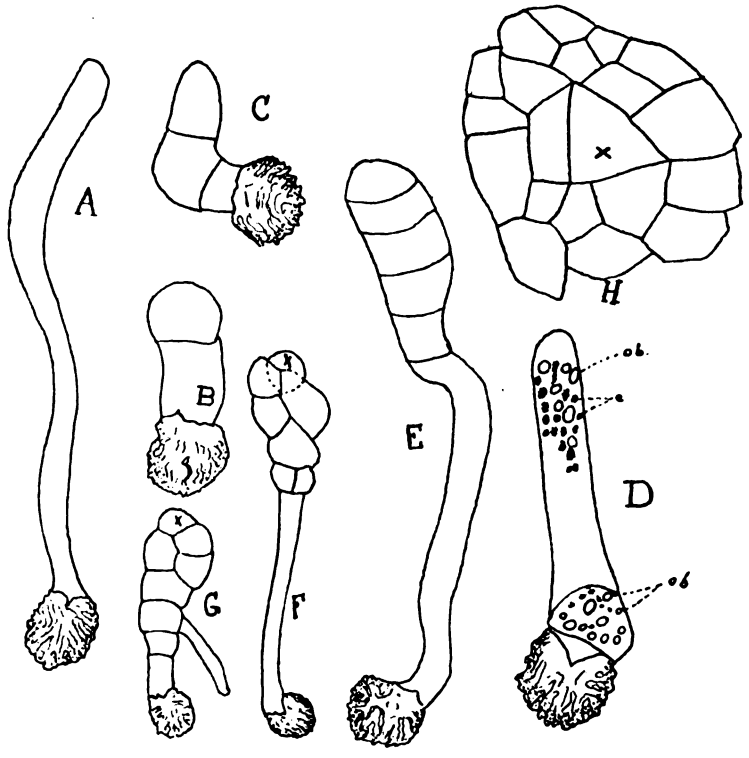

FIG. 4. A. A young plant grown on a soil-culture. × 300. B, C, and D. Young plants grown in water-cultures. × 300. D. Young plant containing within its cells numerous oil-bodies (*ob*) and chlorophyll grains (*c*). × 300. E. Young plant grown on a soil-culture. Twelve days old. × 300. F and G. Young plants in which the 'two-sided' apical cell (*x*) has appeared. Young rhizoid seen in the latter. × 112. H. Cross-section of apical point of an old plant. × 560.

none germinated in the tap-water till the nineteenth day. In a later tap-water-culture spores germinated in about half that time. After eleven days the young plants had reached a stage represented in Fig. 4, C and D. It was thought probable that spores germinating in the various water-cultures might show a tendency towards the development of a longer germ-tube than occurs in plants grown on soil, but in no water-culture did a germ-tube become longer than the one represented in Text-Fig. 4, B. Spores sown on sterilized soil germinated much more readily. In one culture

the first appearance of a germ-tube was recorded six days after sowing, but this was in a culture started in November. In May, 1904, a quantity of mature capsules were collected, and cultures of spores were started early in June on sterilized earth. These were kept in light of as near the normal intensity as possible, covered with a bell-jar which served to sustain an even condition of moisture. Spores in this culture did not germinate until late in August, and in no great numbers until the middle of October. This would seem to support the theory that, in all these forms, the spores necessarily have to pass through a certain resting period before germination. In a later study the writer intends investigating this point with reference to a number of Archegoniates, as it seems to be a somewhat mooted question as to whether the resting period is a constant character.

Text-Fig. 4, A represents a young plant grown on a soil-culture. Here an unusually long, unsegmented germ-tube has been developed, while Fig. 4, E and F represent young plants of the same culture twelve days old. In Fig. 4, D segmentation occurred at at early stage followed by a second division-wall, thus cutting off a short cell from which developed a germ-tube of considerable length. It would seem that this early segmentation is hardly to be considered as normal, since in nearly every case a germ-tube of some considerable length develops prior to any division into cells. Furthermore, in the water-cultures in which the sporelings were subject more or less to the injurious influence of the Bacteria unavoidably present, early division occurred in the majority of cases.

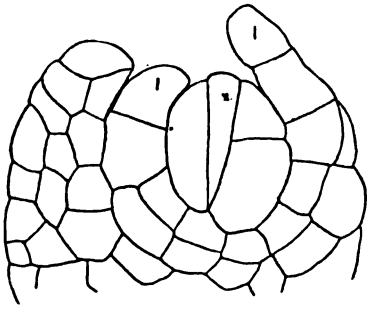

FIG. 5. Horizontal section through growing point of stem. Apical cell *x*, leaves 1, 1. × 560.

On the first appearance of the germ-tube it is seen to contain a very few chlorophyll-bodies, but is rich in oil-globules. As the plant advances these diminish in number, though to no great extent. Thus far the early development of *Fossombronia* agrees essentially with that of *Riccia hirta*, of *Fimbriaria californica*, and of *Sphaerocarpus terrestris*, var. *californicus*, as reported by Campbell [1]. As in *Riccia*, the axis of growth is continuous with that of the germ-tube, and at an early stage (Fig. 4, F and G) the regular two-sided apical cell appears, from which a rapid growth ensues. This apical cell occurred repeatedly in young plants of about the age of those represented in the above figures. As in *Geothallus* [2], leaf-like lobes are seen to appear in some cases on either side of the apical cell. The leaves

[1] Campbell ('95), Mosses and Ferns, p. 38.

[2] Campbell ('96), vol. x, p. 506.

develop from lateral segments as described by Leitgeb [1] for *F. pusilla.* The apical growth of the species was carefully worked out by him, and it agrees in all essential particulars with that of *F. longiseta.*

Along the ventral surface, just behind the growing point, certain cells resulting from the divisions of the primary or inner segment of the apical cell, elongate to form glandular hairs. As a rule these are void of chlorophyll, but contain numerous oil-bodies. However, a very few have been noticed in which a few chlorophyll-bodies were present, though in a state of disintegration.

The first rhizoid, as a rule, appears rather late in the development of the young plant, though in Fig. 1, B and Fig. 4, G it is seen arising from the third cell. In a single instance it was seen to develop from the first or basal cell. It appears as a delicate, thin-walled, almost colourless structure, usually containing one or more granules and oil-globules. In one instance a number of chlorophyll-bodies were present. Young plants grown in water-cultures produced rhizoids quite as freely as those growing on soil, which fact suggests that after all the rhizoid may be other than an organ of mere attachment. To be sure it may be said that in the appearance of rhizoids on plants grown in water-cultures we have nothing more than the manifestation of the *hereditary tendency* of the plants to develop rhizoids. We are not certain that such a *tendency* is an actual fact, and until further and more conclusive light has been thrown upon this subject it will be unsafe to say positively what is the function of a rhizoid. Of the fact that it serves as a hold-fast we are certain, and the writer has found that stimulation due to continued contact has led to a more or less extensive branching of rhizoids in *Aneura* and *Cephalozia.*

The growing rhizoid of *Fossombronia,* not unlike the root-hairs of higher plants, contains protoplasm in contact with the inner surface of the rhizoid wall, and it would appear from this that there must be osmotic interchange between rhizoid and the outside medium. Peirce [2] considers the rhizoid as the physiological equivalent of the root-hair, hence an absorbing organ. Whether or not it is such can be demonstrated only after further experimentation and study.

It is an interesting fact that, so far as the writer's observations go, the earlier rhizoids are quite colourless, the characteristic vinous-purple rhizoids appearing after one or more pairs of leaves have developed. In a few instances young rhizoids, 50 to 70 μ in length, have been observed, containing along with oil-globules some chlorophyll, which later breaks down and disappears. These could not possibly have been glandular hairs, as the vinous-purple colour was already present. Very likely the chlorophyll had migrated into the rhizoid from the basal cell previous to the formation of the separating wall.

[1] loc. cit.

[2] Peirce ('03), p. 115.

The Antheridium.

The antheridia occur singly or in groups of two to four along the dorsal surface of the stem or near the bases of the leaves. They are spherical or somewhat oblong in outline, and are attached by means of stalks of variable length, though normally equal to the diameter of the antheridium-body. The stalk is composed of four rows of cells, and is slightly inclined to the plane of the stem surface of the thallus. Mature antheridia first appear as pale yellow or as orange-coloured organs, this change of colour being due to the breaking down of the chlorophyll in the wall-cells, and, to a certain extent, to the large mass of mature spermatozoids within. The antheridia are devoid of any envelope, thus differing from *Geothallus* or *Sphaerocarpus*, plants which in many respects resemble *F. longiseta*. In *Fossombronia* the antheridia mature in some instances within three weeks after growth of the thallus is resumed, and they appear in increasing numbers until about January 1, after which time their normal development ceases. Under certain unusual climatic conditions, such as have prevailed in California during the past winter and spring, antheridia have gone on developing and maturing in considerable numbers throughout the entire season. This, however, is to be considered as quite abnormal, and may be accounted for by the excessive late rains, and warm winter and early spring temperature.

The antheridia arise from single dorsal cells of the younger dorsal segments. In this respect their origin agrees with that of the antheridia as described by Campbell [1] for *Sphaerocarpus* and *Riccia*, and by Leitgeb [2] for *F. pusilla*.

Developing as they always do at the base of a leaf which in its early growth extends over the antheridium, there is thus afforded a protective covering to the young organs beneath. By the time the antheridium is nearly mature the leaf has unfurled, leaving the antheridium exposed to a normal amount of light and moisture. The initial cell of the antheridium is somewhat larger than the neighbouring vegetative cells, and is readily distinguished from them by its deeper staining qualities, no doubt accounted for by the somewhat larger nucleus and denser protoplasm. Just previous to the first division the initial cell becomes considerably elongated, extending a third or more of its total length above the surrounding cells. The first division results from the formation of a horizontal wall which cuts off the stalk from the antheridium itself. Unlike what occurs in the majority of the Jungermanniaceae, the next division, instead of being vertical, is horizontal, thus dividing the antheridium mother-cell into two superimposed cells, whereas in *Sphaerocarpus* [3] and *Geothallus* [4] another horizontal wall is formed, thus producing another cell, the two uppermost

[1] Campbell ('95), Mosses and Ferns, p. 79.
[2] loc. cit., Heft 3, p. 110.
[3] Campbell ('96), vol. x, p. 497.
[4] id.

dividing vertically to form the antheridium, while the basal cell, by a series of transverse walls, forms the foot.

In *Fossombronia* the development thus far agrees exactly with that in *Sphaerocarpus* and *Geothallus*, except that in *Fossombronia* only one horizontal division occurs in the antheridium-mother-cell, the stalk arising from the basal cell formed by the first horizontal division. This basal cell later divides horizontally, the uppermost segment becoming active in the formation of the stalk, while the lower ordinarily does not divide again. Following the horizontal division of the antheridium-mother-cell are two vertical

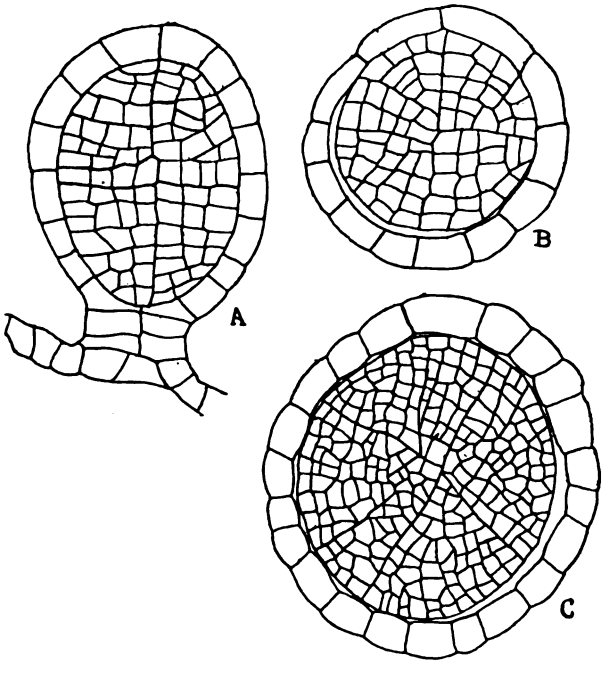

FIG. 6. A. Longitudinal section of a young antheridium. × 560. B. Cross-section of one about the same age. × 560. C. Cross-section of a nearly mature antheridium, primary divisions still evident. × 560.

divisions forming planes at right angles to each other and dividing the antheridium into octants (Figs. 5 and 6, Pl. V). The next division results in periclinal walls for each of these octants, and there thus arise eight central cells and eight periclinal ones. The resulting divisions of the octant cells occur with considerable regularity, developing sperm-cells which are nearly perfect cubes. The primary divisions remain visible up to the early stages of spermatogenesis. Judging from the development of the antheridium, *Fossombronia* is more closely related to *Sphaerocarpus* and *Geothallus* than to the higher forms of the Jungermanniaceae. Leitgeb[1], in his

[1] loc. cit., Heft 3, p. 112.

description of *F. pusilla*, states that in this species the development of the antheridium does not in any way differ from that of the normal type for the Jungermanniaceae. Thus it seems that *Fossombronia longiseta* forms a connecting link between such forms as *Sphaerocarpus* and *Aneura*. The discharge of spermatozoids was observed under the microscope, and was found to resemble closely that occurring in *Porella*[1]. The cells composing the antheridium-wall are quite hygroscopic, and within a few seconds following the addition of water, those at the top of the antheridium, which appear to be somewhat larger than the others, separate and roll outward, followed in rather rapid succession by the cells below (Fig. 13 *a*, Pl. V). Many of the cells are several times longer than broad, and when distended become markedly U-shaped. The form assumed by the cells on absorbing water seems to aid materially in pulling them apart, just as in *Porella*, though in a less marked degree. As the antheridium opens, the mature spermatozoids stream out, and within twenty to thirty seconds the antheridium is empty. The ripe spermatozoids soon become free and swim about actively.

Spermatogenesis.

Up to the present time a number of investigators have studied the development of spermatozoids in the Hepaticae and have given more or less complete accounts[2]. Among the most comprehensive are the studies of Schottländer[3], Guignard[4], Strasburger[5], and the recent and exhaustive work of Ikeno[6] on the spermatogenesis of *Marchantia polymorpha*. The development of spermatozoids in *Fossombronia*, while in many respects agreeing with Ikeno's account[7], presents, on the other hand, some interesting differences. Mitosis in the spermatogenous tissue of half- or two-thirds-grown antheridia was studied in a number of stages and does not differ in any way from the mitosis of the spermatid mother-cell. The nucleus, at first relatively small and almost hyaline, enlarges rapidly as it approaches the spirem stage and a considerable amount of chromatin appears. At the same time the nuclear membrane becomes apparently much thicker, but this seems due to the presence of chromatic material and to the cytoplasm, which at this stage is quite granular. The nucleolus is large and conspicuous, but as the prophase advances this structure appears to become more or less vacuolate, as described by Farmer[8] for *F. Dumortieri* in the mitosis of the sporogenous cells. The most careful study of the

[1] Campbell ('95), p. 101.
[2] Campbell ('87), Bd. v, p. 120.
[3] Buchtien ('87), Heft 8.
[4] Le Clerc du Sablon ('88), p. 876.
[5] Schottländer ('92).
[6] Guignard ('89), p. 1.
[7] Strasburger ('92), Heft 4.
[8] Ikeno ('03), Bd. xv, pp. 65–68.
[9] id. ('03), Bd. xv, Pl. III, Figs. 1, 9, 10.
[10] Farmer ('95), vol. ix, Pl. XVI, Fig. 4.

nucleus at this stage failed to reveal anything that might be interpreted as a centrosphere or a centrosome. In this respect *Fossombronia* certainly appears to differ from *Marchantia polymorpha*, for which Ikeno has figured a well-defined centrosome appearing first among the linin threads, afterwards moving to the surface of the nucleus from which it is discharged. It was thought most likely to appear, if present at all, at the time of elongation of the nucleus just prior to the development of the spindle, but here again the protoplasm surrounding the nucleus disclosed the presence of nothing that could be considered a centrosome. The protoplasm about the nucleus presents a rather homogeneous granular appearance, and it is barely possible that this may account for the failure to observe centrosomes were they present.

The various stages of mitosis are passed through quite rapidly, and intermediate stages between the spirem and mature spindle were not observed, consequently it is not known what structures, if any, are instrumental in bringing about the polarity of the spindle. In *Marchantia polymorpha* Ikeno figures the centrosome as active in spindle-formation, the two exerting an opposed pull upon the cytoplasm after the nuclear membrane has extended in the direction of the centrosomes and has made contact with them.

However, since no centrosome or homologous structure was seen in either of the above-named or antecedent stages, it is probable that the spindle develops in much the same way as in *Anthoceros*, where centrosomes are not known to exist.

Successive divisions of the spermatogenous tissue occur, in which the cells seem, so far as observed, to divide simultaneously, though in one antheridium all the cells in one-half of the section were in early prophase, while those in the remaining half were in metaphase. Up to the division resulting in the formation of the spermatid cells the divisions take place so as to form nearly cubical cells which are normally quite regular, following, as can be seen in many cases almost to the last division, the original lines of the primary and early divisions. Fig. 14, Plate V represents mature cells of an antheridium about two-thirds of the way along in its development. Fig. 16, Plate V represents similar cells of an antheridium just preceding the first of the last two-divisions, at which time the antheridium has attained nearly its mature size. Here we notice a considerable decrease in size as the cells divide, and it would seem that the growth of the antheridium does not parallel the increase in the number of cells [1].

After a number of successive and regular divisions in the spermatogenous tissue, the antheridium is divided into a greatly increased number of cells which undergo a final division to form the spermatid cells.

[1] Peirce ('08), pp. 165-6.

According to Ikeno[1] the spermatid mother-cells divide diagonally, thus forming spermatids of triangular outline without the formation of a wall between them. This is true of *F. longiseta* and *Aneura* as well as other Liverworts thus far observed. Each one of the spermatids thus formed develop later into spermatozoids. Up to the division of the spermatid mother-cell, all divisions are at right angles or nearly so, with the spindle lying in the long axis of the cell. In the spindles of a number of these cells the number of chromosomes could be estimated, and so far as could be ascertained they are eight.

In the case of the diagonal division (division of spermatid mother-cell) the axis of the spindle is invariably diagonal, thus dividing the cell into two daughter-cells, whose greater faces are parallel as in Fig. 23, Pl. V. As mentioned above, no division-wall is formed between these two daughter-cells, which appear to be nothing more than regular masses of protoplasm supplied with nuclei and surrounded at first by a delicate membrane, which later becomes a more evident structure. Thus inside of the spermatid mother-cell, which Ikeno also refers to as a 'tesserale Zelle,' are developed these two nucleated bodies or spermatids.

The method of division in the spermatid mother-cell is the same as that described above for other cells of the antheridium. In one or two cases bodies were seen at or near the poles of a spindle, that, so far as location goes, might have been interpreted as centrosomes, but were in all probability protoplasmic granules; for here again none of the nuclei in the spirem or prophase conditions exhibited structures such as occur at corresponding stages in *Marchantia*. The diaster phase of division was not observed in the mitosis of the spermatid mother-cell, but appeared a number of times in the younger spermatogenous cells. After the completion of mitosis in the spermatid mother-cell, the two daughter-cells (spermatids) contract, drawing away from the wall of the mother-cell though still preserving their original form for some length of time.

In *Marchantia polymorpha* Ikeno[2] reports the disappearance of the centrosome at the completion of mitosis in the cells of the younger spermatogenous tissue, reappearing in the early spirem stage of the next division. While in the division of the spermatid mother-cell he figures a centrosome just outside of each daughter-nucleus, instead of within as in preceding divisions. This centrosome[3], he states, remains unchanged up to the time it assumes the function of a blepharoplast.

In *Fossombronia* no evidence of such a structure can be seen in the daughter-cells: in fact, not for some time after the contraction of the cell-contents of the newly formed spermatids do the blepharoplasts appear. These bodies may be made out with considerable ease, as they take up the

[1] loc. cit. ('08), p. 73, Fig. 17 of plate. [2] loc. cit., p. 71, Fig. 166 of plate.
[3] loc. cit., p. 86.

stain with marked avidity. In all cases examined the blepharoplast first appears in the cytoplasm, but no light can be thrown upon its origin. Much time was devoted to the study of this particular question, but without result. Shortly after the appearance of this structure it is seen to migrate towards the more acute angle of the spermatid, which in some cases faces the similar angle of the sister cell, though usually they are seen to lie as represented in Fig. 24, Pl. V. At the completion of migration the blepharoplast is seen to occupy the angle above mentioned, and appears closely applied to the cell membrane. Previous to this, however, there also appears in the cytoplasm another and considerably larger, dark-staining body, reported for the first time in the Hepaticae by Ikeno in his studies on the spermatogenesis in *Marchantia polymorpha.* It seems that Strasburger and Guignard have not reported such a structure in the plants studied by them. To this body Ikeno gives the name 'Nebenkörper.' Its behaviour in the spermatid of *Fossombronia* is somewhat different from that in *Marchantia.* It appears in the cytoplasm, Fig. 26, Pl. V, without reference to any definite position, though usually it is found occupying a position not far from the nucleus and between the nucleus and the blepharoplast, which, by the time of the appearance of the 'Nebenkörper,' has nearly completed its migration to the pole. Invariably this accessory body seems to seek a position just beneath the blepharoplast, where it is seen to elongate. Ikeno[1] states that shortly after the cilia have started to grow the 'Nebenkörper' in *Marchantia* vanish. Thus, according to his description, this structure plays no part in the formation of the spermatozoid, though his figures seem to show an elongation of the 'Nebenkörper,' and the ultimate passage of the same into the structure of the spermatozoid, apparently forming the middle piece. Further on, however, he states (p. 79) 'der cytoplasmatische Forsatz beginnt sich auszubilden und wächst nach der Richtung des vorderen Endes des jetzt sich bildenden Spermatozoids hin, um schliesslich das Zentrosom zu erreichen, so dass dieser Forsatz den letzteren mit dem Zellkern verbindet.' In *Fossombronia* several preparations were obtained, showing the attenuation of the 'Nebenkörper' as represented in Fig. 29. At this stage, Fig. 30, Pl. V, or a little before, the cytoplasm is seen to elongate in the direction of the 'Nebenkörper' and blepharoplast, apparently connecting with the former, which in its elongated form has come to lie close to the plasma-membrane of the young spermatozoid. Later the connexion seems to become complete as in Fig. 31, Pl. V, and then the developing spermatozoid elongates rapidly. Previous to the appearance of cilia the blepharoplast elongates somewhat (though a number of instances were observed in which this was not perceptible), apparently following the inner contour of the cell-membrane instead of forming a 'Cytoplasmahöcker' as described by

[1] loc. cit., p. 71.

Strasburger [1] for *Pellia calycina*. However, owing to the extreme minuteness of the organ in question, it is not impossible that the blepharoplast of *Fossombronia* grows out into a hook-like process as in *Pellia*. The cilia, in nearly all cases where they could be seen, were closely applied to the cell-membrane, and this position they retain throughout development.

As the body of the spermatozoid elongates, the chromatin of the nucleus appears to condense, and ultimately conceals the nucleolus (Fig. 31, Pl. V), which up to this time has been more or less apparent. This condensation is followed by an elongation of the nuclear chromatin, which seems to connect with the chromatic substance of the elongated 'Nebenkörper.' The spermatozoid when mature shows about one and a half complete turns of a spiral. The two cilia are relatively about as long as those in other Jungermanniaceae, and in the coiled mass of the spermatozoid are closely applied to the body.

In *Marchantia polymorpha* Ikeno describes an abnormal division of the spermatid into two rounded cells, each of which later becomes a spermatozoid. The division is amitotic, resulting in two 'Nebenkörper'; and a little later the 'Zentrosom' divides, followed by division of the nucleus. Nothing of this nature was observed to occur in *Fossombronia*. Ikeno [2], along with Hirase [3], Belajeff [4], and a few other investigators, holds the view that a genetic relation exists between the centrosome and blepharoplast, as opposed to the view of Webber [5], Strasburger [6], Mottier [7], Shaw [8], and others, who see no good reason why one should be considered homologous with the other. Mottier is of the opinion that the radiations of the blepharoplast primordium, described by some authors, is the only evidence they can produce in support of such an homology. According to Ikeno, the 'Zentrosom' appears constantly throughout the mitosis of the spermatogenous tissue of *Marchantia*, while Shaw and Belajeff describe the blepharoplast as first appearing in the 'grandmother' cells. In *Fossombronia* these, if they previously exist, are not evident until after the completion of division of the spermatid mother-cell, at which time they are easily made out lying in the cytoplasm not far from the nucleus. Bearing this in mind it is difficult to understand why, when employing exactly the same methods, these blepharoplasts, if present, did not appear during the divisions prior to the formation of the spermatid cells. Mottier, judging from evidence at hand, holds the opinion that the blepharoplast arises in the cytoplasm *de novo*, and the writer's studies regarding *Fossombronia* seem to support this view.

In so far as the preparations show, the 'Nebenkörper' in *Fossombronia*

[1] loc. cit., pp. 128–9.
[2] loc. cit., p. 77.
[3] Hirase ('98), vol. xii, pt. 2.
[4] Belajeff ('99), Bd. xvii.
[5] Webber ('01), p. 77.
[6] loc. cit.
[7] Mottier ('04), p. 47; loc. cit., p. 49.
[8] Shaw ('98).

arise *de novo*, and as above stated do not disappear as described for *Marchantia*. Shaw[1], in his studies on *Marsilia*, represents in Fig. 5 a body lying about midway between the spindle and cell-membrane, which he names a blepharoplastoid. This, as it appears in his Fig. 2, Ikeno[2] considers as recalling that stage of the 'Nebenkörper' in *Marchantia*, as he has represented it in his Fig. 35. Whether the two are in any way homologous, only continued study can reveal. In fact, this whole question as to the origin of the 'Nebenkörper' and its morphological and physiological significance is one upon which only the study of many Archegoniates can throw any helpful light.

The writer's work on *Fossombronia*, while agreeing in many essential respects with what occurs in *Marchantia* and *Pellia* and certain Ferns that have been investigated, still presents some important differences which bespeak the great need of continued work along the same line with a large number of forms.

The Archegonium.

The development of the archegonium shows a few peculiarities, but in its more essential features it agrees with the other Hepaticae. It arises in a manner not unlike that of the antheridium, and in its initial stage, Fig. 37, Pl. VI, is sometimes difficult to distinguish from the first stage of the antheridium. Usually, however, it does not extend so far above surrounding cells. The first division, being horizontal, divides the initial cell into the archegonium-cell proper and the stalk. The upper cell is usually considerably larger than the lower, differing in this respect from *Sphaerocarpus*[3]. The next division in all cases examined did not take place in the stalk-cell, as in *Sphaerocarpus* and *Geothallus*[4], but in the upper cell, where a nearly vertical wall is formed (Fig. 30, Pl. VI) very much as in other Liverworts. This is followed by two similar divisions in the remaining larger cell, thus separating the archegonium-cell into four. Following this, the stalk-cell divides by a horizontal wall, and later on a vertical division occurs.

A horizontal division near the top of the axial cell cuts off (Fig. 41, Pl. VI) a central cell, that later divides horizontally forming a canal-cell and an egg-cell. Thus the axial row comes to consist of three cells, the upper of which constitutes the cover-cell. About this time two of the three peripheral cells divide vertically, thus forming five neck-cells, Fig. 46, Pl. VI, the typical number for the Jungermanniaceae. In a few instances, however, cross-sections revealed six neck-cells as in *Geothallus*[5], Fig. 47, Pl. VI, and in the Marchantiaceae.

[1] loc. cit. ('98). [2] loc. cit. [3] Campbell ('95), p. 76.
[4] Campbell ('96), pp. 500–1 [5] loc. cit.

The number of neck-canal-cells is, so far as observed, invariably six (Fig. 45, Pl. VI). The mature archegonium is considerably more enlarged through the venter than in *Porella*, and the egg-cell is noticeably larger than the central canal-cell in comparison with *Porella*, corresponding more nearly with these cells in *Sphaerocarpus*. The cells constituting the wall of the venter consist usually of one layer, though Text-Fig. 7, A, represents a case where two layers occur. Here again *F. longiseta* differs from *F. pusilla* as described by Leitgeb [1], where, according to him, the ventral wall is commonly two layers of cells in thickness. The development of the perianth, as described by him, agrees exactly with that of *F. longiseta*, in that it develops only after fertilization, the unfertilized archegonium bearing at its base only a chain or two of cells resembling somewhat glandular hairs. The perianth is always open anteriorly and grows much more rapidly than the young sporogonium, completely hiding it until nearly ripe.

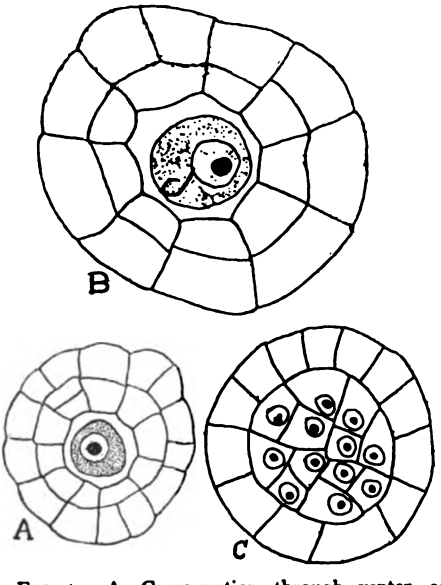

FIG. 7. A. Cross-section through venter of mature archegonium. × 560. B. A similar section showing presence of spermatozoid in the egg. × 1200. C. Cross-section of young embryo. × 560.

The unfertilized egg has a well-defined receptive spot. The relatively large egg-nucleus, as well as the nuclei in other parts of the plant, as a rule possess but one nucleolus and a small amount of chromatin. Text-Fig. 7, B, represents a fertilization stage in which the spermatozoid has entered the egg-cell. Later stages were not obtained.

The neck of the mature archegonium, owing to retarded growth on one side, is always more or less curved and inclined, as are the antheridia, to the plane of the thallus. Usually a number of archegonia develop, but only in rare cases are more than one of these fertilized. Fig. 1, Pl. V, represents a plant on which two sporogonia have developed, and that, too, from parts of the thallus where one would least expect them. Usually the development of the sporogonium marks the end of the season's growth for the plant. It is usually situated just behind the growing point instead of far back on the thallus as in Fig. 2, Pl. V.

[1] loc. cit., p. 113.

THE EMBRYO.

The first division in the embryo is transverse, dividing the considerably enlarged egg-cell into two nearly equal ones, Text-Fig. 8, A, the epibasal cell later giving rise to the capsule and seta as in the typical Jungermanniaceae, and the hypobasal portion giving rise to the rather conspicuous foot. Following the primary division there next occurs a transverse wall in the epibasal cell, dividing it into two, the uppermost evidently giving rise to the archesporium, and lower one the seta.

There next occurs a third transverse division, this time dividing the epibasal cell into two, the lower one commonly dividing no further until

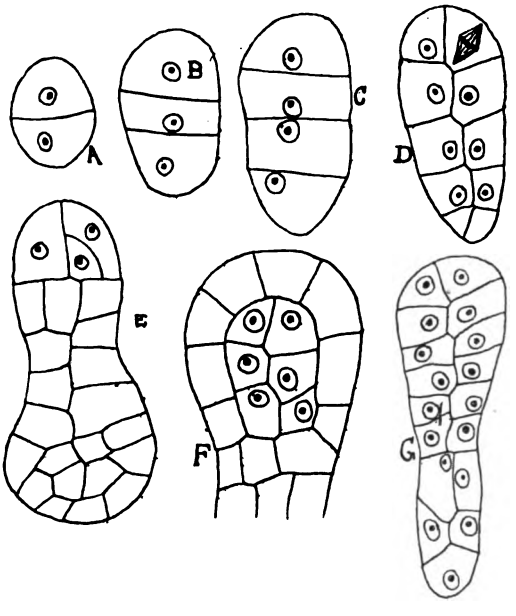

FIG. 8. A–D. Successive stages in development of the embryo. × 560. E. Differentiation of archesporium and formation of first periclinal wall. × 560. F. A later stage in development of archesporium. × 560. G. An abnormal embryo. × 560.

the embryo has reached an advanced stage, Text-Fig. 8, C. The embryo now consists of a tier of four superimposed cells, and the next division, Fig. 8, D, is a vertical one, followed by another at right angles to the first, thus dividing each cell into four parts. In the upper or archesporial cells are now formed periclinal walls, thus separating four archesporial cells from four wall-cells, Fig. 8, E, the initial layer of the capsule-wall. By this time a number of rather irregular divisions have occurred in the lower half of the embryo, along with an increase in size in the archesporial region, and, owing to the slow development of the stalk, the characteristic dumb-bell shape is already evident.

Further transverse divisions, followed by vertical ones, occur in the archesporium with considerable regularity, as seen in Text-Figs. 8, F, and 7, C. In *Fossombronia pusilla*, according to Leitgeb [1], the somewhat elongated egg divides by transverse walls into three cells, and then occur vertical divisions in both the end-cells, resulting in the rather rapid development of the capsular and foot regions. Further than this the two species agree in the development of the embryo. The archesporial cells rapidly increase in number, completely filling the space of the capsule. Several slides were obtained showing the early stages in the development of the elaters and spore-mother-cell. Fig. 50, Pl. VI, shows a group of archesporial cells where cells of different sizes are shown. In Fig. 53, Pl. VI, a later stage is shown, where the difference between the spore-mother-cells and the elater-initials has become very pronounced. In the latter the cell-contents seem to have contracted and elongated, while the spore-mother-cells are more regular in outline and the greater mass of cell-contents has drawn away from the cell-wall into a more spherical body, which ultimately forms the spore-tetrad. The original cell-walls persist for some time, being still faintly perceptible at the time of tetrad-formation, but finally breaking down.

The mitosis of the sporogenous cell was carefully studied and found to agree with Farmer's [2] account of the same in *F. Dumortieri*, with the exception of a failure to find centrospheres at any stage. Structures in a few cases were present that resembled vague radiations, but these also bore a resemblance to an irregular streaming disposition of the cytoplasm at either pole of the nucleus, as in Fig. 50, Pl. VI. Very prominent asters have been figured by Garber [3] for *Ricciocarpus natans*, and it is possible that by using his methods they will be found to occur in *F. longiseta*. Anything like a complete series of satisfactory stages in the formation of spores has not yet been obtained for this species. As stated by Farmer, the sporogonia at the time of mitosis in the spore-mother-cell are fixed with great difficulty. The utmost care was employed throughout the whole process of fixation, dehydration, and embedding, but the exceedingly interesting and important matter of the mitoses that occurs in the spore-mother-cell remains a subject for subsequent study.

Stages just preceding the appearance of the spindle in the first mitosis were obtained, which are of interest here. Previous to any change in the nucleus, which usually occupies an approximately central position in the mother-cell, instead of lying in one lobe of the cell as described by Davis [4] for *Pellia*, the wall of the spore-mother-cell constricts at four opposite points as figured by Farmer [5] for *F. Dumortieri*, Davis for *Pellia*

[1] loc. cit., vol. iii, p. 117.
[2] Farmer, Ann. Bot. ('95), vol. ix, pp. 470–1.
[3] Garber, vol. xxxvii, Fig. 35.
[4] Davis, vol. v, xv.
[5] loc. cit.

and *Pallavicinia*, and Moore [1] for *Pallavicinia*. Following this the nucleus, in which the nucleolus is relatively very large, shows a delicate, reticular structure and assumes an equi-four-angled form (Fig. 55, Pl. VI). Here again no radiations were perceptible, although different stains were employed. In one case the anilin-safranin—gentian-violet—orange *G* combination was employed, but more satisfactory results were obtained with the iron haematoxylin, using erythrosin as a contrast stain. A little later the nuclear protuberances are considerably elongated, extending well into each lobe of the cell. At this stage there seems to appear an accumulation of cytoplasm at the four poles, but nothing like definite radiations could be made out. At this time in all cases examined the nucleolus had begun to undergo change, in some instances appearing vacuolated, while two of the nuclear arms were somewhat longer than the others, which corresponds with Farmer's account of the spore-mother-cell nucleus in *F. Dumortieri* just preceding the appearance of the bipolar spindle. Satisfactory stages of the further behaviour of the nucleus were not obtained, so we pass to the events following mitosis. The ultimate outcome of the division in the spore-mother-cell is the tetrad, each cell of which has it own nucleus, equaling in size that of the archesporial cell, though the nucleus is relatively smaller than is true of the spore-mother-cell. Protoplasmic granules in the cytoplasm lie disposed irregularly, giving the protoplasm a somewhat vacuolated appearance. Each spore now becomes surrounded by its own proper wall, and a little later a distinct endospore becomes differentiated. Judging from its staining qualities the old spore-mother-cell wall becomes mucilaginous, and by breaking down the spores become liberated within the capsule, in which respect it agrees with the other Jungermanniaceae, with the exception of *Sphaerocarpus*. The spores have already been described by Howe [2] as showing considerable variation in external appearance, which leads him to think that this is significant of a possibility that we may be including under the head of *F. longiseta* more than one species. The writer's investigation can throw no light upon this point. He has found the echinate and cristate types of spores produced on plants that in no other respects appeared to differ. In the majority of cases the inner faces of the spore are nearly smooth in comparison with the outer face; the cristate ridges of the latter, at times, apparently being continuous near the limits of the inner faces, as seen in Fig. 59, Pl. VI.

Normally the spores are somewhat compressed and round-tetrahedral in outline, measuring from 38 to 50 μ in greatest diameter. The ripe sporogonium by the rapid, and relatively very great, elongation of the seta reaches a total length of 10 to 16 mm. For some time previous

[1] Moore, vol. xxxvi, Fig. 1 of plate.
[2] loc. cit., p. 82.

to the growth of the sporogonium above the involucre the capsule is already very dark-brown or black, and to all appearances the spores are ripe.

The capsule bursts in a manner characteristic among the Jungermanniaceae, splitting irregularly into four valves which turn back, exposing the mass of spores and elaters. The development of the elaters parallels in rate that of the spores, the spiral thickening appearing at about the time of the differentiation of the spore-crests. In a few cases much deformed nuclei were observed in elaters, in which the double spiral band was very prominent, but in the fully mature elater all trace of such a structure seems obliterated. Judging from its appearance at different stages in the development of the elater it undergoes structural changes that render it incapable of differentiation by use of stains, and, though it may still be present in the mature elater, it is not recognizable from other bodies sometimes present upon the inner surface of the wall. The mature elater attains a length varying from 150 μ to nearly twice that length.

The capsule-wall is normally bistratose, the cells of both layers commonly bearing incomplete annular-like thickenings, though, in the original description of the genus, these thickenings are described as occurring only in the cells of the inner layer. In the material used in the preparation of this paper the wall in many cases appeared as in Fig. 64, Pl. VI, in which it is readily seen that the development of these bands is by no means as constant a character in the outer cells as in those of the inner layer, and might quite easily be overlooked.

Viewed *en face*, these annular bands appear as in Fig. 63, Pl. VI, and are by no means as regular as those described by Cavers[1] for *Preissia commutata*, *Targionia hypophylla*, and *Monoclea Forsteri*. The calyptra, previous to the ultimate elevation of the capsule, is very closely applied to it, in fact so closely does it fit over the capsule as to make it sometimes difficult to distinguish its individuality from the capsule-wall-cells themselves. As soon as the seta begins to lengthen the calyptra ruptures, thus exposing the nearly ripe capsule.

The foot, somewhat globular in form, attains a relatively greater size than the corresponding structure in *Sphaerocarpus*. Its basal outline is irregular, owing to the development of cells that project (Fig. 62, Pl. VI) half or more of their diameter beyond the average limits of the foot. The cells of the foot, especially those in the basal portion, are very rich in granular protoplasm, each possessing a conspicuous nucleus as in *Geothallus*[2]. In all cases examined the foot gives evidence of a considerable growth and consequent compression of the proximate cells of the gametophyte.

[1] Cavers ('04), pp. 9, 33, 44.

[2] Campbell ('96), p. 504.

SUMMARY.

1. The apex of each leaf-lobe terminates in a single, smaller cell, void of chlorophyll, though always containing a few oil-globules and considerable mucilaginous fluid. These cells bear a strong resemblance to the mucilaginous hairs, and are, doubtless, of the same physiological significance to the plant.

2. The plants are susceptible to great desiccation without material injury. On being moistened they revive in a few hours. Plants that have passed through a dry season are often found bearing sex-organs in an advanced stage of development.

3. The germinating spore produces normally a germ-tube of considerable length, containing little chlorophyll, but rich in oil-globules, which diminish in number as the growth of the young plant advances. The segmentation of the germ-tube shows variation, sometimes taking place very early, as in Text-Fig. 4, D. The first rhizoids commonly appear at a later stage; these are colourless, while those of older plants are vinous purple.

4. The antheridium mother-cell divides once horizontally; this is followed by a horizontal division in the basal cell, the uppermost segment of which becomes active in forming the stalk. Following horizontal division of the mother-cell are two vertical divisions, giving rise to octants. Further divisions in the spermatogenous tissue occur with marked regularity.

5. The development of the antheridium in *Fossombronia longiseta* shows it to have a certain morphological relationship with such forms as *Geothallus* and *Sphaerocarpus*.

6. No centrosome was observed at any stage of nuclear division in spermatogenesis. The spermatid mother-cell divides to form two spermatids, between which no wall is formed.

7. Blepharoplasts appear apparently *de novo* in the cytoplasm of the spermatid. These migrate to one of the spermatid poles and later develop cilia.

8. A 'Nebenkörper' appears in the cytoplasm of the spermatid, and migrates towards the pole occupied by the blepharoplast. Here it elongates and appears to connect up with the cytoplasm and blepharoplast, thus forming the middle piece of the spermatozoid.

9. The mature sperm forms a spiral of about one and one-half turns.

10. The first division in the archegonium-mother-cell is horizontal, followed by three nearly vertical divisions in the upper cell. This is followed by horizontal and vertical divisions in the stalk-cell. Later divisions result in the formation of cap and axial-cells. The latter divide to form six canal-cells, a ventral canal-cell, and relatively large egg, bearing a well-defined receptive spot.

11. The number of neck-cells is normally five, though occasionally six.

12. The first division in the embryo results in two nearly equal cells. From the epibasal portion arise capsule and seta, the hypobasal cell giving rise to the foot.

This division is followed by another horizontal one in the epibasal cell, separating capsule and seta initials.

Another horizontal division in the hypobasal cell leaves the embryo consisting of four superimposed cells.

13. Vertical divisions now occur, giving rise to four cells from each initial, with the exception of the foot-cell, which does not divide till much later.

14. Periclinal walls now appear, one for each archesporial quadrant. This is followed by further divisions, occurring most frequently in the foot and archesporium.

15. The seta is commonly about seven cells in diameter, and elongates but little till maturity of spores.

16. The archesporial cells divide rapidly, forming, ultimately, elater-initials and spore-mother-cells. The spores develop in tetrads, separating before rupture of capsule-wall.

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EXPLANATION OF FIGURES IN PLATES V AND VI.

Illustrating Mr. Humphrey's paper on *Fossombronia longiseta.*

PLATE V.

Except when otherwise indicated, all drawings were made from microtome sections, and were drawn with the aid of an Abbé camera lucida. All sections were stained with Flemming's triple stain, except when otherwise stated.

Fig. 1. A thrice dichotomous plant bearing three sporangia, natural size.

Fig. 2. A plant bearing antheridia and archegonia. × 10.

Fig. 3. A mature plant bearing a single sporogonium. × 10.

Fig. 4. Initial cell of antheridium in which the first division has occurred. × 560.

Fig. 5. A later stage in the development of the antheridium in which a second horizontal division has occurred and the first vertical wall is in process of formation. × 560.

Fig. 6. Octant stage. Two vertical walls have formed at right angles to each other as indicated in Fig. 9, cross-section of an antheridium of same stage. × 560.

Fig. 7. Stage in which periclinal walls have formed. × 560.

Fig. 8. Cross-section of stage represented in Fig. 5. × 560.

Fig. 9. Cross-section of stage represented in Fig. 6. × 560.

Fig. 10. Cross-section of stage represented in Fig. 7. × 560.

Figs. 11 and 12. Cross-sections of later stages. × 560.

Fig. 13. A mature antheridium drawn shortly before discharge of spermatozoids. Crown cells much swollen. × about 300. Ad. nat.

Fig. 13*a*. An antheridium that has discharged its spermatozoids. × 150.

Fig. 14. Spirem stage of nucleus in cells of spermatogenous tissue of very young antheridium. × 2400.

Fig. 15. Diaster stage of mitosis in cells of a somewhat older antheridium. × 1750.

Fig. 16. Spirem stage of nucleus in cells from which the spermatid mother-cells arise. Stained with iron haematoxylin and safranin. × 2400.

Fig. 17. Metaphase in division of cells of the age of those represented in Fig. 16. Stained with Flemming's triple stain, also with iron haematoxylin. × 2400.

Fig. 18. A spindle viewed *en face* showing chromosomes. × 2400.

Fig. 19. A group of spermatid mother-cells; nuclei in resting-stage, though the chromatin is appearing and the nuclei are about to pass into the spirem condition. No blepharoplast apparent. Stained with iron haematoxylin and safranin. × 2400.

Fig. 20. Spirem stage of spermatid mother-cell. Stained with Flemming's triple stain. × 1750.

Fig. 21. Metaphase of mitosis in spermatid mother-cell. × 1750. Stained with iron haematoxylin and safranin.

Fig. 22. Formation of spermatids within spermatid mother-cell; line of separation indicated between them. × 2400.

Fig. 23. Separation of spermatids, and appearance of a blepharoplast in cytoplasm of each cell. × 2400.

Fig. 24. Migration of blepharoplasts to opposite poles. × 2400.

Fig. 25. Migration of blepharoplasts to like poles. × 2400.

Fig. 26. First appearance of 'Nebenkörper' in cytoplasm. × 2400.

Figs. 27 and 28. Migration of 'Nebenkörper' towards blepharoplast. × 2400.

Fig. 29. Elongation of 'Nebenkörper' near blepharoplast from which cilia have developed. × 2400.

Fig. 30. Elongation of cytoplasm in direction of the 'Nebenkörper.' × 1750.

Fig. 31. Further elongated cytoplasm which has apparently connected up with the 'Nebenkörper' which is thus forming the middle piece of the spermatozoid. × 1750.

Fig. 32. Condensation of the nucleus and elongation of spermatozoid. × 2400.

Fig. 33. A later stage in the growth of the spermatozoid. × 2400.

Fig. 34. Mature spermatozoid still within matrix. Stained with gentian violet. × about 1800.

Figs. 35 and 36. Free spermatozoids. × about 1800.

PLATE VI.

Figs. 37–44. Successive stages in development of archegonium. × 560.

Fig. 45. Mature archegonium in which a well-marked receptive spot is seen in the egg. × 560.

Figs. 46 and 47. Cross-section showing number of neck-cells. × 560.

Fig. 48. Spirem stage of nucleus in archesporial cell. Nucleolus still present. × 1750.

Fig. 49. Spirem stage of nucleus of similar cell in which nucleolus has disappeared. × 1750.

Fig. 50. A group of archesporial cells in one of which a mature spindle is figured. × 1200.

Fig. 51. Anaphase, in archesporial mitosis.

Fig. 52. Formation of daughter-cells. × 1750.

Fig. 53. A group of sporogenous cells among which have appeared elater initials. The larger cells are spore-mother-cells. × 650.

Fig. 54. Initial stage in the formation of a spore-tetrad. × 560.

Fig. 55. A later stage in which the nucleus is elongating into each lobe.

Figs. 56, 57 and 57 *a*. Spore-tetrads and elater of same age. × 560.

Fig. 58. Section through spores of a tetrad about to separate. Mucilaginous wall between and around them. × 560.

Fig. 59. A ripe spore. × 560.

Fig. 60. A mature elater and median section through a ripe spore. × 560.

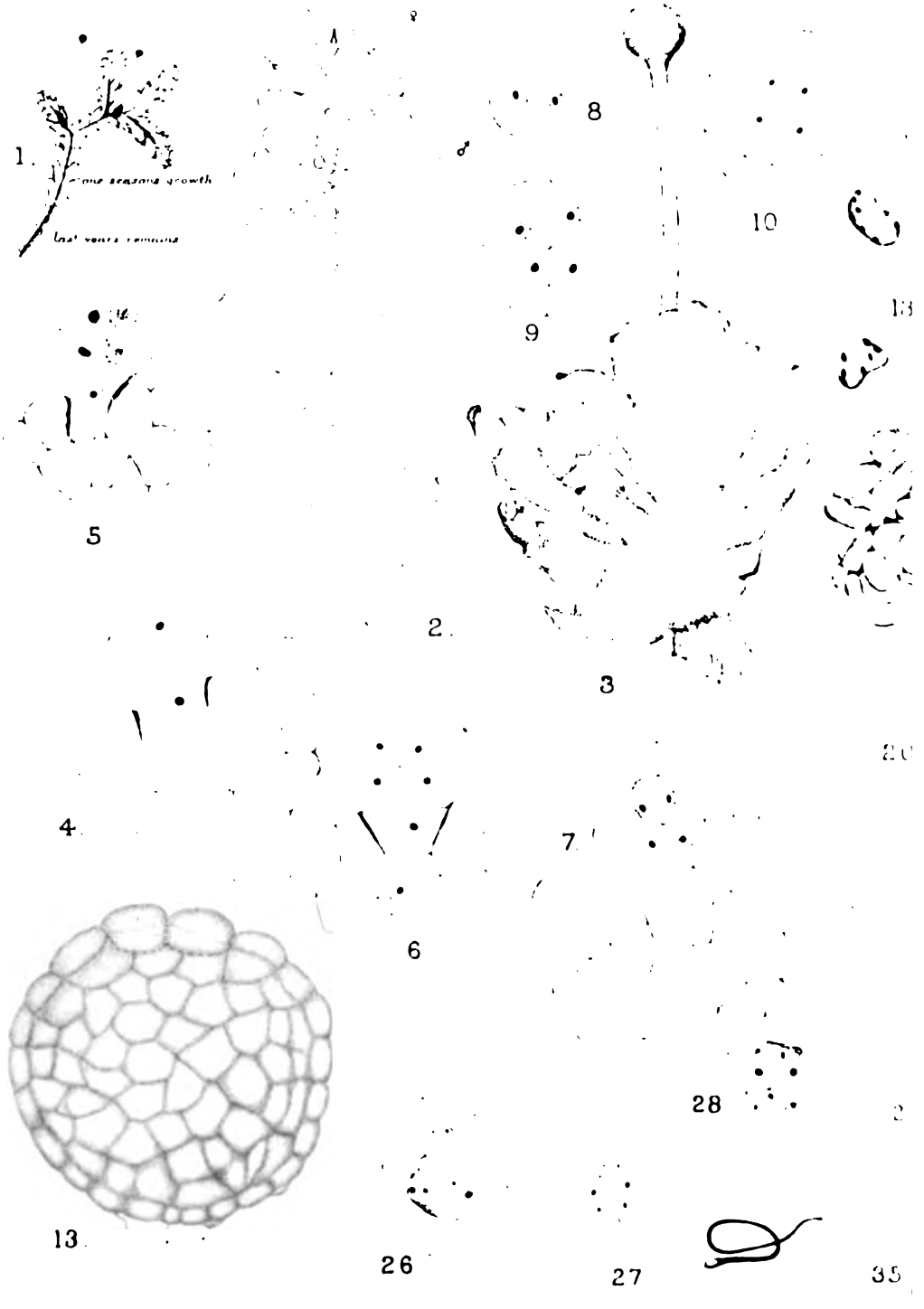
Fig. 61. Diagram of a longitudinal section of sporogonium just previous to elongation of the seta. × 80.

Fig. 62. Median longitudinal section through the foot. × 335.

Fig. 63. View of a portion of inner surface of capsule wall showing annular thickenings. × 560.

Fig. 64. View of capsule wall seen in longitudinal section of capsule. Showing annular bands in cells of both layers. × 560.

Fig. 65. Spindle in cell of gametophyte. × 1200.



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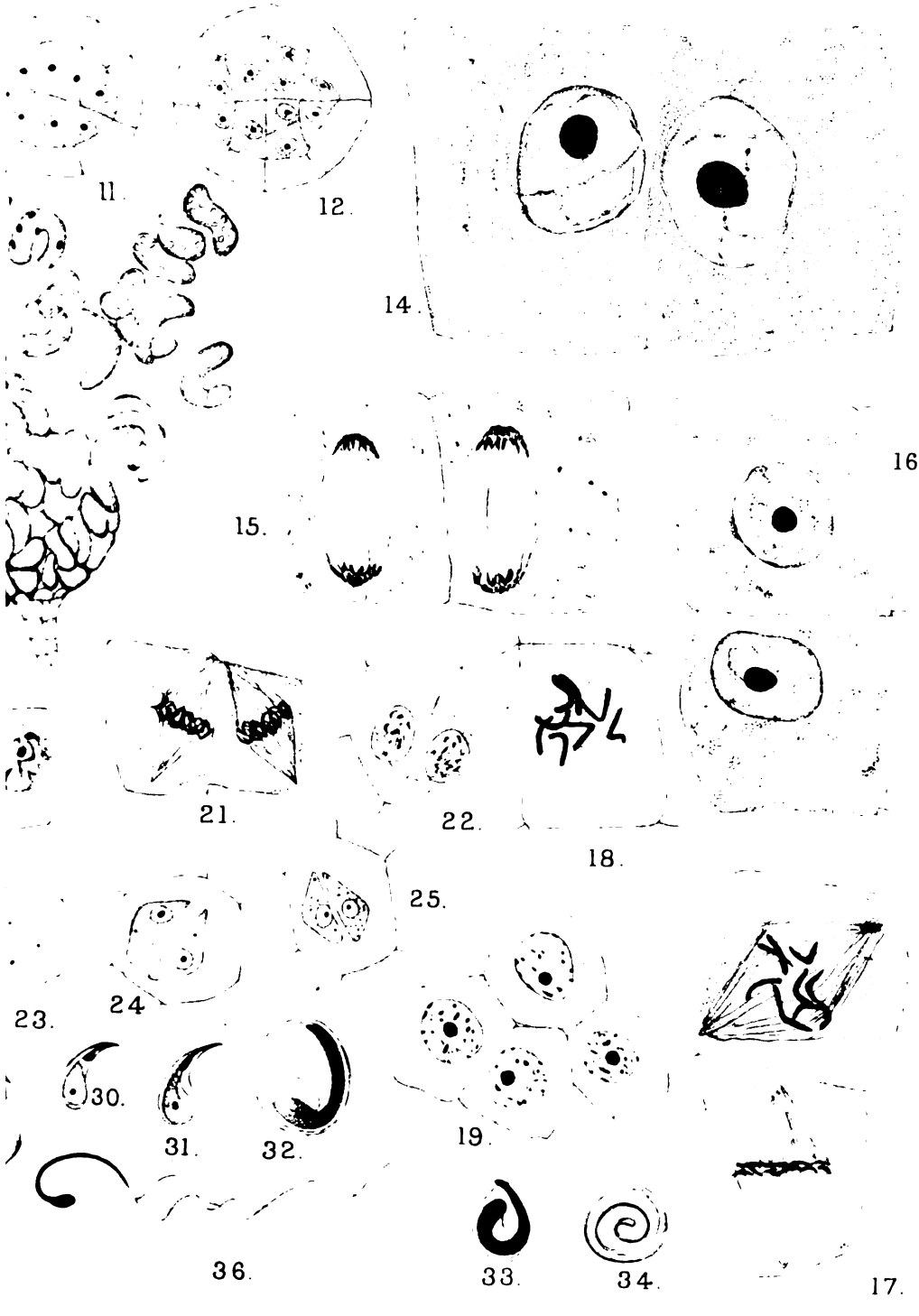

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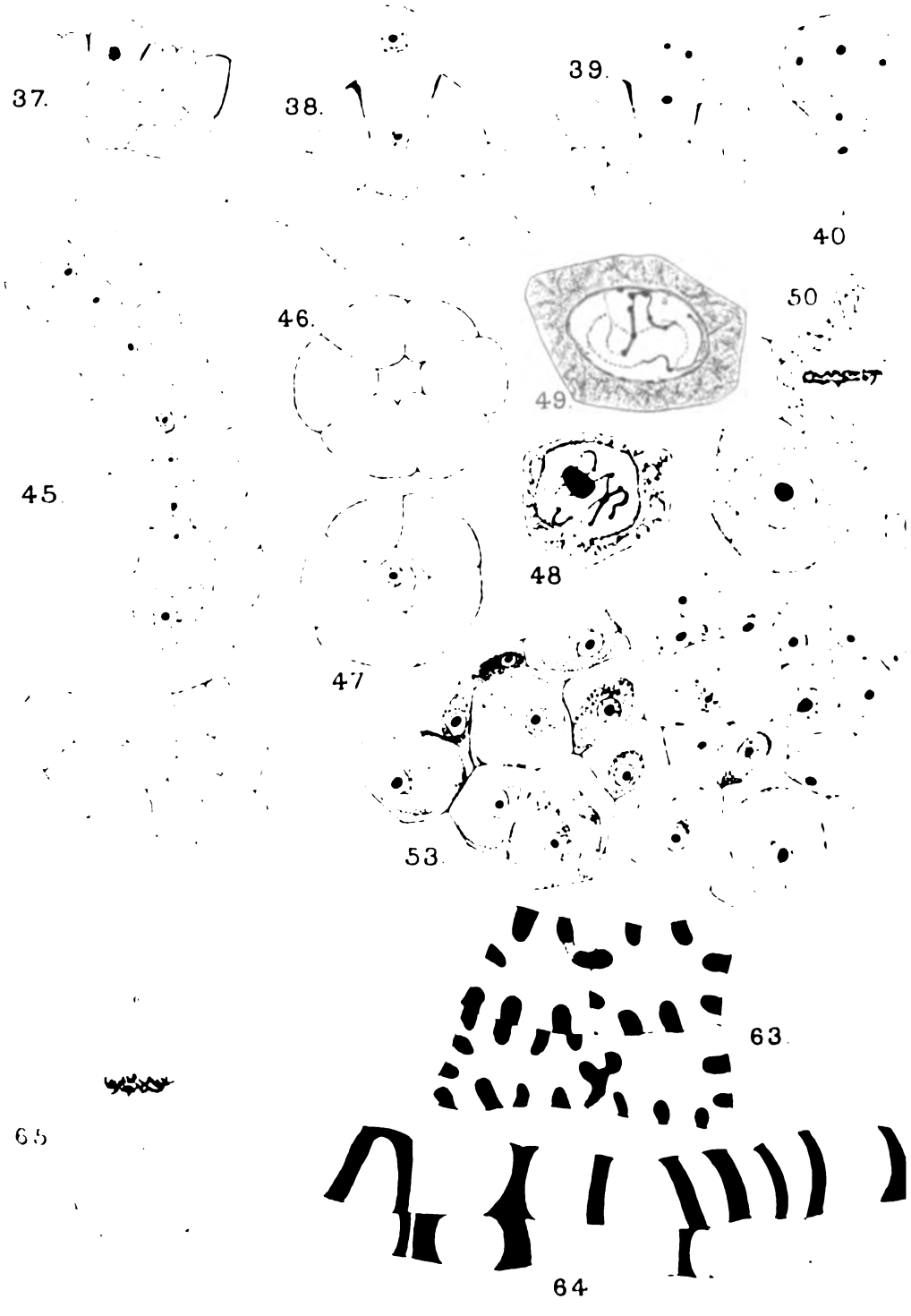

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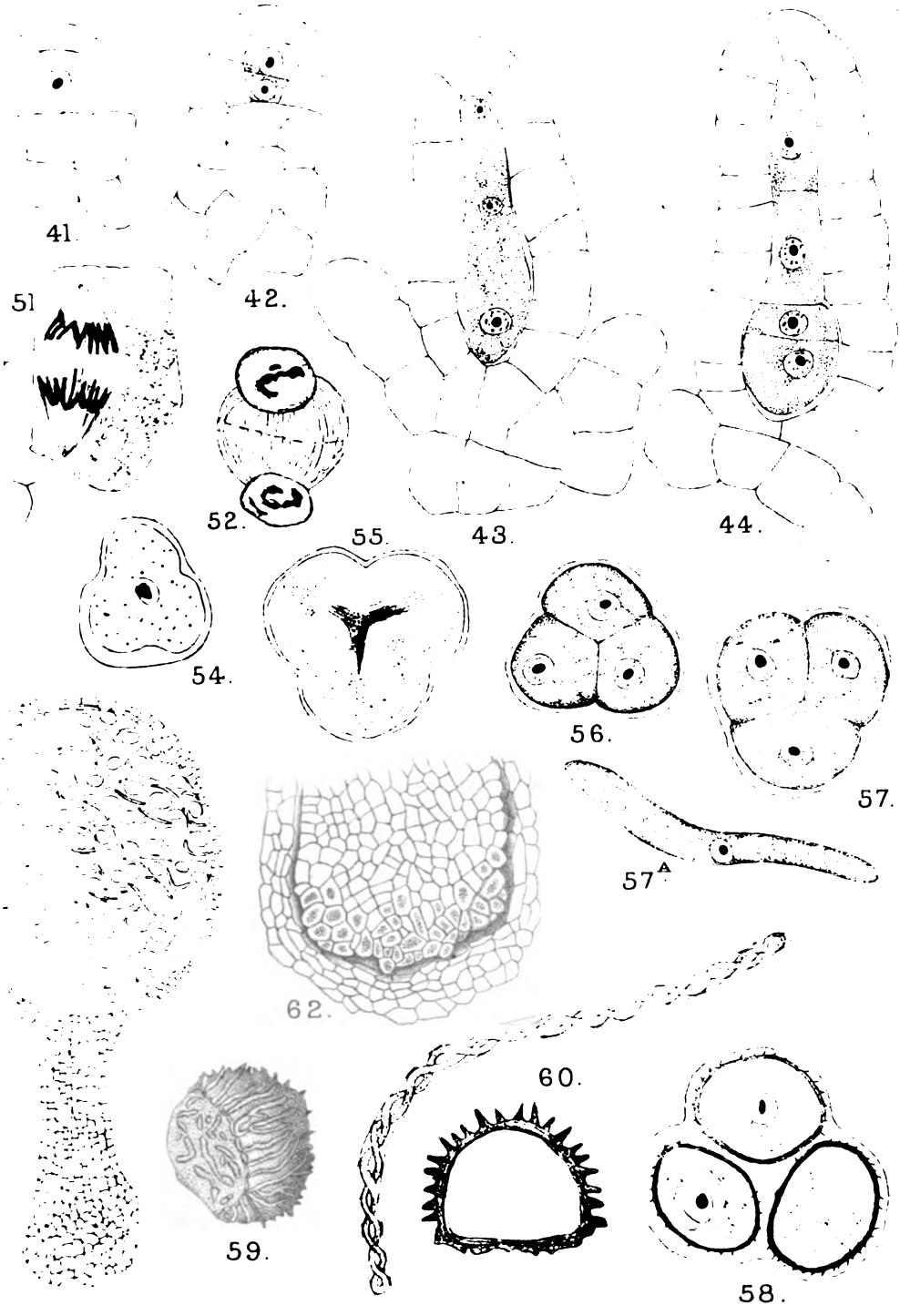

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NOTE.

NOTE ON THE STRUCTURE OF TRIGONOCARPON OLIVAEFORME.—The seed with which the present preliminary note is concerned will be spoken of provisionally by the name *Trigonocarpon olivaeforme*, familiar to palaeobotanists from the work of Williamson. The question of the specific relation of the petrified specimens under consideration to the seeds preserved as casts, will be left open at present.

The structure of *Trigonocarpon* was first described by Hooker and Binney in 1855 [1], and subsequently by Williamson in 1877 [2]. From the works of these authors a good knowledge of the more general features in the anatomy of the seed has been obtained. Much more recently, in 1900, the late Mr. George Wild published an interesting paper [3] dealing chiefly with the structure of the micropylar region and of the outermost layers of the testa, and in 1904 [4], Prof. F. W. Oliver gave an account of the French petrified specimens of *Trigonocarpus pusillus* originally described by Brongniart. Our own work is entirely based on specimens from the British Coal-Measures, which appear to be at least specifically distinct from the French forms.

In the present note, without entering further into the literature of the subject, we propose to give in the first place a short general account of the structure of the seed, and then to place on record the chief results of our own investigations, leaving a more detailed and illustrated description, as well as any theoretical points involved, for a later opportunity. *Trigonocarpon olivaeforme*, which is not uncommon in the calcareous nodules of the Lower Coal-Measures of Britain, is a large seed of ovate form, the body of the seed commonly measuring at least 20 mm. in length by 16 mm. or more in its greatest diameter. The general transverse section is approximately circular and radially symmetrical, so that *Trigonocarpon* is a typical member of the Radiospermeae of Prof. F. W. Oliver [5]. The micropylar region was of great length, fully equal to that of the body of the seed, so that a full-sized specimen when complete would have measured from 40 to 50 mm. from end to end. This is shown, for example, in a fine specimen of the complete seed (*T. Parkinsoni*), in the Hutton Collection at Newcastle [6].

[1] On *Trigonocarpons* contained in nodules of Limestone. Phil. Trans., vol. cxlv, p. 149.

[2] Organization of Fossil Plants of Coal-Measures, Part VIII, Phil. Trans., vol. clxvii, p. 248.

[3] On *Trigonocarpon olivaeforme*, Trans. Manchester Geological Society, Part XV, vol. xxvi.

[4] On two Palaeozoic Seeds, *Trigonocarpus* and *Polylophospermum*, New Phytologist, vol. iii, No. 4.

[5] Structure and Affinities of *Stephanospermum*, Brongniart. Trans. Linnean Soc., vol. vi (Botany), 1904.

[6] Figured in Lindley and Hutton, Fossil Flora, Pl. 87, Fig. 3; Photograph in Scott, Wilde Lecture, On the Early History of Seed-bearing Plants, Memoirs and Proceedings Manchester Literary and Philosophical Society, vol. xlix, 1905. Pl. III, Fig. 4.

The seed, as is well known, possesses a very thick two-layered testa, the inner zone of which, the endotesta or sclerotesta, consists of sclerotic tissue many cells in thickness; its more external elements are commonly elongated in the radial direction. The sclerotesta bears three sharp and prominent longitudinal ridges on its outer surface with corresponding furrows on the inner side, marking the position of the three sutures; in each space between two main ribs are two, or more commonly three, less prominent ridges, the whole number of projections thus varying from nine to twelve. The degree of prominence of the various ridges is very variable; in some cases only the three main ribs are clearly marked. The thickness of the sclerotesta between the ridges is about 1–1·25 mm.

On the outside, the sclerotesta is abruptly succeeded by the delicate tissues of the sarcotesta, the inner layers of which consist of a continuous thin-walled parenchyma, passing over towards the exterior into a lax tissue, with large and definite lacunae between the cells. This zone, owing to its weak construction, is seldom well preserved, and its usually collapsed condition prevents us from giving any accurate estimate of the total thickness of the sarcotesta in the natural state, which must certainly have exceeded 2 mm. The lacunar zone had not previously been distinguished. The whole is bounded externally by the limiting layers to which Mr. Wild first called attention. They consist of a hypoderma formed of one or sometimes two series of columnar cells, resembling a palisade-tissue. Beyond this is the true epidermis, composed of small, often nearly square cells. This layer, which had not been noticed before, appears to have been always present, though it is only here and there that it is found well preserved. Mr. Wild compared the limiting layers of the sarcotesta in *Trigonocarpon* as then known (i. e., without the small-celled epidermal layer) with the similar tissues on the exterior of the petiole in *Medullosa anglica*, and indicated the general agreement in structure between the two. It must, however, be pointed out that in the petiole the small-celled epidermal layer has not yet been detected, and it appears that the epidermis itself, as well as the hypoderma, had a palisade-form. The agreement between the two structures thus seems, on our present knowledge, less close than Mr. Wild believed it to be.

The very long micropylar tube, triangular in section in its lower part, is bounded immediately by thick-walled tissue forming the prolongation of the sclerotesta; outside this there is a great development of the sarcotesta, appearing, as seen in the transverse sections, as a wide flat wing on either side of the micropyle (see the series of figures in Mr. Wild's paper). This is limited externally by the usual hypoderma and epidermis. How far the flattened, wing-like form was natural is difficult to determine. There has certainly been some loss of tissue, so that the form in the natural state was less flattened than it now appears. It is doubtful, however, whether in this part of the seed the sectional form could ever have been circular.

One of the principal points to which our attention has been directed, is the distribution of the vascular supply through the seed. We find that there was a double bundle-system present. The outer system is situated in the sarcotesta, the bundles lying opposite the smaller ridges of the sclerotesta; they have

not been found opposite the three main ribs. The bundles are embedded in the inner, denser zone of the sarcotesta. These sarcotestal strands were evidently complete bundles with phloem as well as xylem, and from the best-preserved examples it appears that the xylem was of mesarch structure. The second vascular system of the seed (already observed by Hooker and Binney and by Oliver [1]) runs through the contracted zone of tissue lying between the sclerotesta and the membrane of the megaspore. We regard the tissue in question as representing the nucellus, which appears in this seed, as in *Stephanospermum*, described fully by Prof. F. W. Oliver [2], to have been free from the integument, from the chalaza upwards. In good specimens there is a distinct layer of cells, like an epidermis, limiting the nucellus on the outside, just as is the case at the free tip of the nucellus in a modern Cycad and still more closely resembling the nucellar epidermis of *Stephanospermum* [3]. This specialized layer of cells, which appears to be continuous with the epidermis of the pollen-chamber, can be traced the whole length of the nucellus from the chalaza upwards, and not merely in the upper part as in Cycads. Hence it is clear that the internal vascular system must be regarded as belonging wholly to the nucellus and not to the integument as described by Miss Stopes in *Cycas* [4].

The nucellar vascular system is rather complex in its arrangement. Towards the base, where the nucellar vascular tissue springs from the chalazal strand, it forms for some distance a practically continuous sheath of tracheides; further up the seed the tracheides, which are much flattened tangentially, range themselves in more or less definite but still crowded longitudinal strands, which are connected by transverse anastomoses running in a tangential direction. There is no evidence of phloem in connexion with the nucellar tracheides. The nucellar system has been traced through the whole length of the nucellus almost to the base of the pollen-chamber, and indications of tracheides have been detected even in the beak of the pollen-chamber itself.

The tracheal system of the nucellus springs from the upper end of the chalazal strand, where the latter terminates at the junction of sclerotesta with nucellus. The connexion of the outer, sarcotestal system with the chalazal strand has not yet been traced, but from the position of the bundles, the junction must have been as much as 4 mm. below the base of the nucellus.

The tracheides, especially those of the chalazal bundle and of the sarcotestal strands, show, in longitudinal sections, the fine scalariform markings characteristic of the primary tracheides in *Medullosa*, a point of agreement on which we lay some stress.

The pollen-chamber, already indicated in some of the figures of Hooker and Binney [5], was described and more fully illustrated by Williamson [6]. The pollen-chamber itself forms a wide dome 2·5–3 mm. in diameter at the base. We have to add the new fact that this was provided at the top with a narrow beak or canal, not more than 300 μ in diameter. Curiously enough, this interesting

[1] Structure and Affinities of *Stephanospermum*, p. 391.
[2] Loc. cit. [3] Loc. cit., Pl. XLIII, Fig. 21.
[4] On the Double Nature of the Cycadean Integument, Ann. Bot., vol. xix, Oct. 1905. Beiträge zur Kenntnis d. Fortpflanzungsorgane d. Cycadeen. Flora, Bd. 4, 1904.
[5] Loc. cit., Pl. IV, Figs. 7, 8, and 12. [6] Loc. cit., Pl. XIII and XIV, Figs. 113–115.

structure is best shown in one of the original Hooker and Binney sections, now preserved in the Binney Collection at Cambridge. The presence of a beak is obscurely indicated in the Williamson section (C.N. 1478), shown in Fig. 114 of his Memoir before referred to. The beak, as shown in the Binney slide, is barely half a millimetre in length, but presumably it extended much further in the natural condition. The cells of its outer wall are distinguished by their palisade-form, and there is an inner layer of prosenchymatous elements, apparently of the nature of tracheides. The resemblance to the Cordaitean pollen-chamber as shown in Renault's well-known figure[1] is rather striking, while there is also a fair agreement with the corresponding structures in a recent Cycadean ovule.

The conclusions which we have so far reached as to the structure of *Trigonocarpon olivaeforme* are thus the following:—

1. The sarcotesta was differentiated into an inner, comparatively dense, and an outer, lacunar zone, the whole bounded by a definite hypoderma and epidermis.

2. The nucellus, so far as can be ascertained, was free from the integument throughout its whole length.

3. The pollen-chamber was provided with a beak or canal, comparable to that in Cordaitean and Cycadean seeds.

4. The vascular system of the seed was a double one; the outer system consisting of bundles running free in the sarcotesta, while the inner formed a complex tracheal reticulum in the nucellus, including definite longitudinal bundles, and thus differing from *Stephanospermum* where the tracheal mantle 'is a continuous sheath without trace of local segregation into bundles[2].'

5. The two systems of bundles diverged from the chalazal supply-strand at very different levels.

6. The tracheides agree closely in minute structure with the primary tracheides of *Medullosa*.

The impression that *Trigonocarpon* is the seed of *Medullosa* has been gaining ground for some considerable time, although no evidence of actual continuity is known. The practically constant occurrence of *Medullosa* petioles (*Myeloxylon*) in slides showing *Trigonocarpon*, and the equally general association of the casts of the seeds with the pinnules of *Alethopteris lonchitica*, now known to belong to *Medullosa*, as well as the resemblance in the minute structure of the tracheides, all tend to make the presumption probably true.

Mr. Wild, in his paper before referred to, emphasized the similarity between the outer tissues of *Trigonocarpon* and those of the petiole of *Medullosa anglica*, but, as has been indicated earlier in this note, with our present knowledge, the resemblance does not seem quite as close as he supposed, owing to the apparent absence of the small-celled epidermal layer in the petioles.

It will be best to postpone any discussion of the affinities of the seed, until we are able to publish our work in full.

D. H. SCOTT.
A. J. MASLEN.

KEW.

[1] Tiges de la Flore Carbonifère, Pl. 17, Fig. 15.

[2] Oliver, loc. cit., p. 367.

The Proteases of Plants (IV).

BY

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IN the course of the year 1905 an interesting contribution to this subject was made by Dean, consisting of two papers (1 and 2) on proteolytic enzymes, the principal results of which may be briefly given as follows.

The objects of the investigations detailed in the first paper, as stated by the author, were two: 'in the first place, . . . to test a number of different plant-tissues in order to confirm, if possible, the results of Vines;' whilst 'the second and more important part of the investigation was to make a careful study of the enzymes in some one or two plants.'

With regard to the first object, it is somewhat singular that the author expresses no opinion as to whether or not he succeeded in confirming my results; but it may be inferred from the account of the experiments that he was successful. For instance, in the case of the leaves of the Spinach (*Spinacia oleracea*), his conclusion is that they 'contain an enzyme capable of attacking Witte-peptone, but not acting on the proteids of the tissue, or if it does, these proteids do not yield tryptophan on hydrolysis;' a conclusion which is, on the whole, in accordance with my earlier observation (3) that these leaves act upon Witte-peptone, but are unable to digest fibrin. A similar parallelism exists between his observations and mine on the leaves of the Cabbage (*Brassica oleracea*). Other experiments, made with material that I had not used, the blossoms of the Wild Carrot (*Daucus Carota*), the leaves of the Chestnut (*Castanea sativa americana*), etiolated seedlings of a Bean (*Phaseolus Mungo*), seedlings of *Cucurbita maxima*, gave results supporting the view, which I have expressed more than once, of the widespread, if not universal, occurrence of ereptase in the tissues of plants.

With regard to the second object of Dean's paper, it was pursued by the investigation of the seeds of *Phaseolus vulgaris*, which seems to include the White Haricot Bean and the Scarlet Runner. The result was remarkable. It was found that the cotyledons, whether the seeds were ungerminated or

[Annals of Botany, Vol. XX. No. LXXVIII April, 1906.]

in different stages of germination, contained an ereptase, inasmuch as the material actively digested Witte-peptone as shown by the tryptophane-reaction; but 'at no time could any evidence of the presence of an enzyme capable of attacking the proteids of the seed be obtained.' 'The enzyme acts on the proto-proteose, the hetero-proteose, and the deutero-proteoses, separated from Witte-peptone; it is quite inactive on phaseolin of the bean, excelsin of the Brazil nut, edestin of the hempseed and boiled fibrin.' The author concludes as follows:—'There can be no doubt but that the large proteid store in bean-seeds is utilized in germination, and in all probability this utilization is preceded by cleavage to the amido-acids, hexon bases, &c. What effects this cleavage, and what part, if any, the ereptase plays, are unsolved problems.' It should be noted that the times of digestion mentioned in the various experiments were 41, 19, and 18 hours.

Dean's second paper gives an account of more minute investigations into the chemistry of the seeds of *Phaseolus vulgaris*, with results that confirm the main conclusions of the first paper. He says: 'The results of this study have shown that, as was to be expected, the proteids of the seed undergo proteolysis during germination as a preliminary to the transportation of the nitrogen and its utilization in the formation of new organs. There are three ways in which this process might be carried out: by the action of a tryptic enzyme; by the combined action of the protoplasm and of an enzyme which is, by itself, incapable of carrying out the whole process; or by the action of the protoplasm alone. The results of a study of the proteolytic enzymes of the resting and germinating bean show that there is no enzyme present which is able to digest the proteids of the seed. There is present, however, an enzyme of the ereptase group which is capable of digesting the proteoses resulting from the partial hydrolysis of the seed proteids. It may be, therefore, that the protoplasm of the cells starts the process of proteid decomposition, and carries it to some stage at which the ereptase takes up the work and completes the process.'

Experiments with Seeds.

I turn now to my own observations. Until recently, I had not specially investigated seeds, having only made a few incidental experiments in connexion with the determination of the general occurrence of ereptase in plant-tissues. The first experiments, described in my paper on 'Tryptophane' (4), were made with Malt and with *Vicia Faba*, and showed that extract of Malt readily undergoes autolysis, whereas, in the case of *Vicia*, no autolysis could be detected in 20 hours, though Witte-peptone was more or less peptolyzed in 24 hours. I took occasion to point out at the time that 'the whole subject requires systematic reinvestigation;' and the experiments described in this paper are a first attempt to satisfy that requirement.

In a subsequent paper (3) it was shown that extract of Green Peas (*Pisum sativum*) acts strongly on Witte-peptone; and that the 'germ' of Wheat not only acts upon Witte-peptone, but also digests fibrin. My last paper on proteases (5) contains an account of more detailed investigation of the proteolytic properties of Malt, carried on with the object of elucidating the nature of the enzymes which effect not only peptolysis but also peptonization.

I begin with a general description of the methods adopted. The seeds, as a rule without their integuments, were ground in a hand-mill: in nearly every case 10 grms. of the flour were triturated with 100 c.c. distilled water (10 % mixture): the mixture was generally used as such, but in some cases it was allowed to settle and the supernatant liquid decanted off: the antiseptic was HCN 0·1 %: the ox-fibrin had been preserved in a mixture of dilute glycerin (50 %) and alcohol, and was well washed before an experiment: the mixtures for digestion were put into stoppered bottles to prevent loss by evaporation, more especially of the HCN, a few drops of which were added from time to time when the experiments were protracted: the temperature of the incubator was about 40° C. The fibrin was suspended in the digesting mixture by a thread, so that it could be readily examined from time to time. The fibrin used was of the same stock throughout the whole of the experiments; the fact that in many instances the fibrin was not digested, suffices to remove any suspicion of self-digestion.

The seeds employed were those of the following plants:—*Vicia Faba* (Broad Bean), *Pisum sativum* (Pea), *Phaseolus multiflorus* (Scarlet Runner), *Phaseolus vulgaris* (White Haricot Bean), *Lupinus hirsutus* (Blue Lupin), and *Zea Mais* (Maize). The idea was to compare a number of more or less closely allied seeds, in this case Leguminous, introducing an altogether different one by way of contrast. In every case it was ascertained that the sample of seed used was capable of germinating. The seeds were germinated in a hot-house.

The experiments were designed to determine whether or not (1) autolysis, or (2) fibrin-digestion, took place in the various mixtures.

(1) *Germinated Seeds.*

Vicia Faba. 19 days after sowing: 30 grms. of ground cotyledons extracted for 48 hours with 100 c.c. distilled water, at room-temperature: the extract gave marked tryptophane-reaction: 40 c.c. of the extract decanted off digested 0·2 grm. fibrin within 24 hours in the incubator.

Phaseolus multiflorus. 7 days after sowing: 10 % mixture gave distinct tryptophane-reaction, which became strong after 24 hours in the incubator: the fibrin (0·3 grm.) had begun to break up after 72 hours, and had entirely disappeared in 120 hours.

50 grms. of the same cotyledons were triturated with 200 c.c. distilled water and

left to stand at room-temperature for 24 hours: 150 c.c. liquid were then decanted off, and gave distinct tryptophane-reaction: the fibrin (0·3 grm.) remained unaltered until the seventh day in the incubator, when it was seen to be breaking up, the tryptophane-reaction being strong: the fibrin had disappeared on the ninth day.

Same crop, 13 days after sowing: the 10% mixture of the cotyledons gave marked tryptophane-reaction: after 24 hours in the incubator, the fibrin (0·3 grm.) was partly digested, and the tryptophane-reaction had become strong: 21 hours later, the fibrin had completely disappeared.

Pisum sativum. 6 days after sowing: epicotyls about 1 inch above the soil: the 10% watery mixture of the ground cotyledons gave marked tryptophane-reaction: after 24 hours in the incubator, the tryptophane-reaction had become strong: the fibrin (0·3 grm.) remained apparently unaltered until 72–96 hours in the incubator, when it was found to be attacked: 48 hours later it had disappeared.

Some seedlings of the same crop were left to grow for 5 days more: a 20% watery mixture of the cotyledons was then made, which gave strong tryptophane-reaction, and digested 0·3 grm. fibrin within 24 hours.

Lupinus hirsutus. 4 days after sowing: radicles 1–2 inches long: 10% mixture gave faint tryptophane-reaction: after 24 hours in the incubator, the tryptophane-reaction had become strong: after 120 hours, the fibrin (0·3 grm.) remained apparently unaltered, but had quite disappeared at the end of 168 hours.

Same crop, 7 days after sowing: 10% mixture gave distinct tryptophane-reaction, which had become strong after 24 hours in the incubator: the fibrin was found to be breaking up after 72 hours, and had disappeared by the end of 120 hours.

Same crop, 11 days after sowing: cotyledons green: the 10% mixture gave faint tryptophane-reaction: after 48 hours in the incubator the tryptophane-reaction was found to have become strong and the fibrin to be breaking up: by the end of 96 hours, the fibrin had disappeared.

Phaseolus vulgaris. 8 days after sowing: the epigeal cotyledons were green: 10% mixture gave faint tryptophane-reaction: after 48 hours in the incubator the tryptophane-reaction had become strong, and the fibrin (0·3 grm.) was breaking up: within 72 hours the fibrin had disappeared.

Zea Mais. 4 days after sowing: radicles well developed: ground up entire grains and seedlings: the 10% mixture gave distinct tryptophane-reaction: after 24 hours in the incubator both the tryptophane-reaction and the fibrin (0·3 grm.) were unaltered: 24 hours later the tryptophane-reaction was marked, and most of the fibrin had gone: 24 hours later the fibrin had disappeared.

The results of these experiments are altogether harmonious. In all cases it was found that, after germination,

(1) the cotyledons, or the entire grain (Maize), contained tryptophane;

(2) the amount of tryptophane rapidly increased during the experiment; and,

(3) fibrin was more or less rapidly digested.

The conclusions to be drawn are obviously these. (1) There was present in these germinated seeds an enzyme that produced tryptophane

from the reserve proteids. The fact that, in the leguminous seeds, the original watery mixture of the cotyledons gave relatively weak tryptophane-reaction, which soon became strong under experimental conditions, indicates, no doubt, that tryptophane, like the other amido-acids, does not accumulate in the cotyledons of the seedling, but is distributed to the growing parts. (2) There was present also an enzyme capable of digesting fibrin. It may be fairly inferred that an enzyme that can digest fibrin can also digest the reserve proteids of the seed.

I am quite unable to reconcile my results and conclusions with those of Dean. Far from being unable to obtain evidence 'of the presence of an enzyme capable of attacking the proteids of the seed,' I have never failed to obtain such evidence whenever the seeds were actively germinating and the duration of the experiment was sufficiently prolonged. In endeavouring to account for the contradiction between us, I am inclined to attribute it, in part at any rate, to the relatively short duration of Dean's experiments: this is, I feel sure, the explanation of my own failure to detect autolysis in my first experiments with *Vicia Faba* (see *ante*, p. 114). But I also attribute it, and more particularly, to what seems to me to be a questionable proceeding in his method of testing. I notice that, before applying any test, whether biuret or tryptophane, the digestive mixtures of *Phaseolus vulgaris* were boiled, then acidified with acetic acid and filtered: in no case was the biuret- or the tryptophane-reaction given by a liquid so treated. The facts, so far as I know them, are these. A watery extract of seed of *P. vulgaris* gives good biuret-reaction: if the extract be boiled and filtered, the filtrate still gives a good reaction, indicating the presence (as I pointed out more than twenty-five years ago with regard to seeds generally) of a proteose or phytalbumose: if, however, the extract be boiled and also acidified with acetic acid and filtered, the reaction is hardly perceptible, owing, as I think, to the precipitation of the proteose by the acid. If now a small quantity of tryptophane be present in such a solution, it is not improbable that it might be carried down wholly or in part by the precipitates formed by boiling and by acidification. It is highly probable, that had the tests been applied to the mixtures in question previously to the treatment indicated, both the biuret- and the tryptophane-reactions would have been obtained. Moreover, I found that some of these leguminous seed-extracts did not give the tryptophane-reaction very readily, so that it was necessary to add the chlorine-water gradually and to the extent of as much as 2–3 vols. before it could be decided whether or not tryptophane were present: possibly this detail may have had something to do with the observed results. In any case it is obviously desirable to exhaust all possible modifications in the methods of such a research, before attempting to explain its results by so speculative an hypothesis as that of the direct intervention of the protoplasm in the proteolysis of the seed.

To return to the interpretation of my own results. Peptolysis and fibrin-digestion both took place: but the question remains, were they effected by a single protease of the nature of tryptase; or were they effected by two distinct proteases, the one an ereptase, the other possibly a peptase?

Dean recognizes the presence of ereptase in the seeds of *Phaseolus vulgaris*, and the facts that I have recorded seem to extend this conclusion to the various seeds with which I have experimented. The important point is that, whereas the production of tryptophane was immediate, the digestion of fibrin was delayed, the less so the longer the seeds had been germinating before the experiment. This difference in point of time suggests that two distinct proteases are concerned in the proteolysis of the seed: were both tryptophane-production and fibrin-digestion effected by one and the same enzyme, the two processes should be carried on more nearly *pari passu* than was observed to be the case. However, it is not urged that the results are absolutely conclusive.

With the object of obtaining some more definite answer to this important question, I instituted a series of experiments with ungerminated seeds of the same plants and from the same parcels. I must explain that in some cases the seeds were used *with* their integuments, though I did not observe that this made any material difference. In other respects the methods employed were the same as those already described.

(2) *Ungerminated Seeds.*

The experiments themselves require no special description, and were exactly the same in all cases: so the results may be at once considered.

The 10 % watery mixtures of the six species of seed investigated gave no tryptophane-reaction, to begin with, except in the case of *Lupinus hirsutus*, where a faint reaction was detected. This being so, the development of a tryptophane-reaction, whilst in the incubator, would be evidence of autolysis; and, as a matter of fact, tryptophane was produced in every instance, with various degrees of rapidity, but rather slowly and gradually as a rule, as indicated in the following table compiled from a number of experiments:—

	24 hrs.	48.	72.	96.	120.	144.
Vicia Faba	—	distinct	marked	—	—	strong
Phaseolus multiflorus .	faint	—	marked	strong		
Pisum sativum . . .	faint	distinct	—	marked	strong	
Lupinus hirsutus . .	strong					
Phaseolus vulgaris .	faint	marked	strong			
Zea Mais	faint	distinct	marked	strong		

In every experiment, then, evidence of autolysis was obtained: clearly a protease was present in the ungerminated seeds that could act upon

some constituent of the reserve proteid. But the differences in the rapidity of action remain to be accounted for: they may be due (1) to variation in the amount of enzyme present in the seeds; or (2) to differences in the amount of the digestible proteid stored in the seeds: or perhaps to a combination of these conditions. I have not attempted to go minutely into the matter; but I have made an observation, based upon my earlier experiments with *Vicia Faba*, that throws some light upon it. I have found that 10 % mixtures of the six species of seeds investigated gave in every case a more or less strong tryptophane-reaction within 24 hours when Witte-peptone had been added to the extent of 0·5 %. Undoubtedly these ungerminated seeds all contained sufficient protease: hence the results of the autolysis-experiments indicate an absence, not of the enzyme, but of the particular proteids upon which the enzyme could act, except in the case of the Lupin, where the tryptophane-reaction was developed as rapidly without as with the addition of Witte-peptone. The slow development of the tryptophane-reaction in the other cases suggests a gradual conversion of less tractable reserve proteids, probably forms of proteoses, into others more readily digestible, probably deutero-albumoses and peptones. However, it is impossible to account fully for the differences observed in the proteolysis of these seeds without an adequate investigation of the nature of their reserve proteids; and this I have not attempted. But I may record my impression that the differences in the constitution of the proteid reserves are not so much dependent upon the kind of seed—that is, are not altogether *specific* differences—as upon the degree of ripeness of the seed. It would appear that the more completely ripe the seed, the more intractable are the reserve proteids. This point, again, can only be settled by further investigation: by comparative experiments with seeds at different stages in the process of ripening.

Having thus dealt with the autolysis of ungerminated seeds, the possibility of fibrin-digestion remains to be considered. The experiments on this question were carried on in the same way as those already described for germinated seeds: in every case 0·3 grm. fibrin was suspended in a mixture consisting of 10 grms. seed-flour and 100 c.c. distilled water, with 0·1 % HCN as the antiseptic.

The results were these: in the case of *Vicia Faba*, *Phaseolus multiflorus*, and *Phaseolus vulgaris*, the fibrin showed no appreciable diminution even when, as in one instance, the experiment was continued for 14 days: in the case of *Pisum sativum*, *Lupinus hirsutus*, and *Zea Mais*, the fibrin completely disappeared in the course of several days. Thus, with *Pisum*, the fibrin showed signs of diminution on the ninth day, and had disappeared on the tenth: with *Lupinus*, in one experiment, the fibrin began to break up on the fourth day and disappeared on the fifth; in another experiment, it disappeared on the sixth day: with the Maize, the fibrin was seen to be

breaking up on the seventh day, and had disappeared on the eighth. Thus it was found that the mixtures of the ungerminated seeds of the Pea, the Lupin, and the Maize, gradually acquired, under experimental conditions, the capacity for digesting fibrin. I cannot explain why this capacity was not equally developed in *Vicia Faba*, *Phaseolus multiflorus*, and *Phaseolus vulgaris*: I can only suggest that in these cases the process is slower, and that possibly fibrin-digestion might have been observed had the experiments been more prolonged.

The probability of the suggestion made in connexion with the experiments on germinated seeds, that two proteases are active during germination, is materially increased by these experiments on ungerminated seeds. It is not reasonable to attribute the digestion of the fibrin, which took place five to ten days after the experiment had begun, to the protease in the resting seed that was found to digest Witte-peptone within a few hours: for if this protease were capable of digesting fibrin, why was its action so long delayed? It is more in accordance with the observed facts to conclude that the ungerminated seeds contained, to begin with, an ereptase but no protease capable of digesting fibrin; and that, in certain cases, such a protease was gradually developed in the course of the experiment.

It occurred to me that it might be possible to accelerate the fibrin-digestion by chemical means; and, with this object in view, I made some experiments in which the distilled water was replaced in the mixtures by NaCl-solutions. The attempt did not prove successful, but the experiments are nevertheless worth mentioning. In the first set, 5 % NaCl-solution was used: the result was that in most cases (*Vicia Faba*, *Phaseolus vulgaris*, Pea, Lupin) the fibrin completely disappeared within 72 hours. This seemed to be satisfactory, but there was the possibility that it might be due, wholly or in part, to solvent action of the salt; and, as a matter of fact, it was found, in a control-experiment, that 0·3 grm. fibrin was completely disintegrated, though not altogether dissolved, when digested for three days in 100 c.c. 5 % NaCl-solution alone, with 0·1 % HCN. In a second set of experiments, a 2·5 % NaCl-solution was used, with the result that the fibrin disappeared in about ten days in the case of the Pea and of the Lupin, but not in any of the Beans (the Maize was not tried), a result which is much the same as that obtained when distilled water was used. It may be added that digestion of 0·3 grm. fibrin with distilled water only, containing 0·1 % HCN, produced no effect though continued for more than a fortnight.

Summary.

The facts established by the foregoing experiments are briefly these:—

(1) The ungerminated seeds were found to contain a protease which acted (*a*) immediately on Witte-peptone, and (*b*) more or less slowly on the reserve proteids of the seeds:

(2) The germinated seeds were found to contain a protease that digested fibrin: this protease was also found in certain cases (Pea, Lupin, Maize) to be slowly developed in the substance of the ungerminated seed in the course of the experiment.

The object of this research was to obtain, from the study of seeds, evidence bearing upon the conclusion at which I had arrived (5) as the result of experiments with Yeast, Malt, Mushroom, and other vegetable substances, that, in those cases in which fibrin-digestion takes place, two proteases are present: the one, essentially peptolysing, ereptase, the other essentially peptonizing, peptase as I believe. The conclusion was based mainly on observations showing that by appropriate chemical means, such as variations in the reaction of the liquid, it is possible to induce differential effects, to retard or inhibit the one process without similarly (if at all) interfering with the other. It is, I consider, definitely supported by the results stated above, which afford evidence of a new kind—the separation of the proteases in point of time. Thus, in the ungerminated seed, one protease only, ereptase, was found to be present, to begin with: no evidence of the presence of the fibrin-digesting protease could be obtained until several days after the experiment had proceeded or germination had been going on.

It must, however, be admitted that all the evidence that I have accumulated does not yet suffice to prove that there is no such thing as 'vegetable trypsin.' One point, at any rate, has become clear, namely, that 'vegetable trypsin' is a mixture of enzymes and that ereptase is one of the constituents. But the nature of the other constituent (or constituents), the fibrin-digesting protease, remains uncertain: it may be a tryptase, but it may also be a peptase. It is not, I think, going too far to suggest that the known facts make the latter suggestion the more probable: to transfer, in fact, the *onus probandi* to those who hold that the enzyme in question is a tryptase.

The general course of proteolysis in the germinating seed can now be intelligibly followed. At first it is confined to the action of the ereptase upon the more digestible reserve proteids such as the proteoses. Within a few days after germination has begun, the fibrin-digesting enzyme is developed: this hydrolyses the higher proteids of the seed, and so produces material upon which the ereptase can continue to act. There does not seem to be any reason whatever for the assumption of the direct intervention of the protoplasm in the process.

List of Papers referred to.

1. Dean: On Proteolytic Enzymes, I; Bot. Gazette, vol. xxxix, May, 1905, p. 321.
2. ——: On Proteolytic Enzymes, II; ibid., vol. xl, Aug., 1905, p. 121.
3. Vines: Proteolytic Enzymes in Plants; Ann. Bot., vol. xvii, Jan., 1903, p. 237.
4. ——: Tryptophane in Proteolysis; ibid., vol. xvi, March, 1902, p. 10.
5. ——: The Proteases of Plants (III); ibid., vol. xix, April, 1905, p. 171.

Morphological Notes.

BY

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With Plates VII-IX.

XI. PROTECTIVE ADAPTATIONS, i.

WE are all so much occupied with exploring and recording what seems to be new that most of us have little time, or perhaps patience, to take stock of the harvest of accurate and acute observation to be found in the writings of authors now almost fallen into oblivion, yet long ago recognized as classical. Such a book is the 'Travels in the Interior of Southern Africa', by William J. Burchell, published in two quarto volumes in 1822–4. Yet the freshness of its outlook and the shrewd appreciation of ideas, which seem to us essentially modern, will amply repay its study. I am told that during the South African war copies were much in request amongst the Intelligence officers, and commanded a high price. Perhaps Professor Poulton, who has charge of Burchell's entomological collections at Oxford and is the vindicator of his zoological work, might induce some enterprising publisher to issue a new edition under his editorship.

MESEMBRYANTHEMUM TRUNCATUM.

The following passage (vol. i, pp. 310–11) recalls the style and feeling of Darwin's 'Naturalist's Voyage':

'On picking up from the stony ground, what was supposed a curiously shaped pebble, it proved to be a plant, and an additional new species to the numerous tribe of *Mesembryanthemum*; but in color and appearance bore the closest resemblance to the stones, between which it was growing. On the same ground was found a species of the *Gryllus* tribe amongst the stones, and so exactly like them in color and even in shape, that it could never have been discovered, had it not been observed just at a moment when in motion; and as if more completely to elude notice, it seldom stirred, and even then, but slowly. The intention of Nature, in these instances, seems to have been the same as when she gave to the Chameleon the

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power of accommodating its color, in a certain degree, to that of the object nearest to it, in order to compensate for the deficiency of its locomotive powers. By their form and color, this insect may pass unobserved by those birds, which otherwise would soon extirpate a species so little able to elude its pursuers, and this juicy little Mesembryanthemum may generally escape the notice of cattle and wild animals.'

Burchell was clearly on the track on which Darwin reached the goal. But the time had not come for emancipation from the old teleology. This, however, in no respect detracts from the merit or value of his work. For, as Huxley has pointed out [1], the facts of the old teleology are immediately transferable to Darwinism, which simply supplies them with a natural in place of a supernatural explanation.

In another passage (vol. i, p. 226), Burchell gets a clear grip of the equilibrium in Nature at which the struggle for existence ultimately arrives. An immediate deduction from this is the utility of specific or at any rate of adaptive characters.

'When we permit ourselves to contemplate the great designs of the creation, all our boasted knowledge of nature appears only as the ideas and the knowledge of children. Too intent on some little parts of the edifice, we often remain totally ignorant of the proportions, and perfect symmetry of the whole. In the wide system of created objects, nothing is wanting, nothing is superfluous: the smallest weed or insect is as indispensably necessary to the general good, as the largest object we behold. Each has its peculiar part to perform, conducive ultimately to the well-being of all. Nothing more bespeaks a littleness of mind, and a narrowness of ideas, than the admiring of a production of Nature, *merely* for its magnitude, or the despising of one, merely for its minuteness: nothing more erroneous than to regard as useless, all that does not visibly tend to the benefit of *man*.'

In a note to the former passage Burchell gives the name *M. turbiniforme* to a new species of *Mesembryanthemum*. I have little doubt that this is the one which he describes in the text. He had, however, apparently been anticipated by Thunberg (see Harvey and Sonder, Flora Capensis, vol. ii, p. 393). Till recently no one seems to have collected it since Burchell, nor as far as I know has it been seen in cultivation in Europe, and it is represented in no published figure.

In 1902 Mr. N. S. Pillans of Rosedale, Rosebank, Cape Colony, a most generous and indefatigable correspondent of Kew, sent both living plants and seeds (which readily germinated) to the Royal Botanic Gardens. The accompanying excellent illustration (Plate VII) is reproduced from a photograph by Mr. E. J. Wallis. The pot was eight inches in diameter and the illustration is therefore slightly less than life-size. Amongst the

[1] See Life and Letters, i, 457.

plants have been placed water-worn pebbles of about the same size from Thames Valley gravel. The plants not merely simulate them in form, but a mottling of the surface also reproduces their weathering. Personally, without referring to the living plants, I am unable, in many cases, to be quite certain which is which.

The *Mesembryanthemum* had two problems to face:—(1) how to minimize the loss of water by transpiration: this is achieved by assuming the spheroidal form with its minimum surface. But (2) as soon as it became a succulent blob it was exposed to the danger of being eaten, and it only escaped this by pretending to be an inedible pebble.

There are some dozen species of *Mesembryanthemum* which form the small group *Sphaeroidea*. In these the vegetative organs have undergone the extreme of reduction and consist in fact of nothing more than a pair of succulent leaves which unite at the top, leaving a mere slit for the extrusion of the flowers. The leaves are from time to time renewed and the old ones shrivel and form a sheathing base to the new pair.

Mr. Pillans obtained the plants which he sent to Kew from the Laingsburg District, which is in the same region as Zandvalley, where Burchell found it.

In the Gardeners' Chronicle for April 7, 1900 (p. 211) there is an illustration from a photograph by Mr. Karl Dinter of another species, *M. truncatellum*, which also simulates 'the stones amidst which it grows,' though I think not so perfectly as *M. truncatum*. Mr. Dinter, however, who found it at Windhook, says from actual observation that it 'so closely resembles, when not in bloom, the form and colour of the pebbles among which it grows, that it can only be detected by an experienced eye' (l. c., p. 115). It is figured in the Botanical Magazine for 1874, t. 6077.

Mesembryanthemum Bolusii.

This case is even more remarkable than the last. The mimicry is with angular rock-fragments instead of water-worn pebbles. It was discovered some time previous to 1877 by Mr. H. Bolus, the well-known South African botanist, and named and described in his honour by Sir Joseph Hooker in the Botanical Magazine for 1882. It has been three times in cultivation at Kew. The first specimens appear to have been promptly stolen; the second not to have survived; for the third we were indebted to Mr. C. J. Howlett, Curator of the Botanic Garden, Graaf Reinet, an old Kew employé, who sent it to the Royal Botanic Gardens in 1903. Sir Joseph Hooker describes technically the pair of leaves which practically compose the plant as 'trigonously hemispherical.' They closely resemble angular stones, of which the weathering is imitated by the 'dull grey-green' surface, and the resemblance is enhanced by the minute pustular

spots with which the surface is studded. These produce exactly the same effect as a minute Lichen (*Lecanora*) on weathered stones.

I exhibited a pan of the plant at a Royal Society conversazione in 1903 and pointed out the resemblance (see Nature, vol. lxviii, p. 185). It was then even more striking than in the accompanying illustration (Plate VIII, from a photograph by Mr. E. J. Wallis), which is half life-size. Since then the plants have produced a second crop of leaves which are still not yet fully developed.

I learn from Nature (vol. lxxi, p. 232) that Dr. R. Marloth has discussed the adaptive resemblances which form the subject of this article in a paper in the Trans. S. Afric. Phil. Soc. (vol. xv, p. 97). Of this I have seen nothing but the brief abstract. He states that *M. Bolusii* grows 'on the rocks round the Karru' and 'closely resembles the surrounding stone, although for a short time its bright yellow flowers render it conspicuous enough.' These are figured from the Kew specimen by Sir Joseph Hooker in the Botanical Magazine, t. 6664.

Anacampseros papyracea.

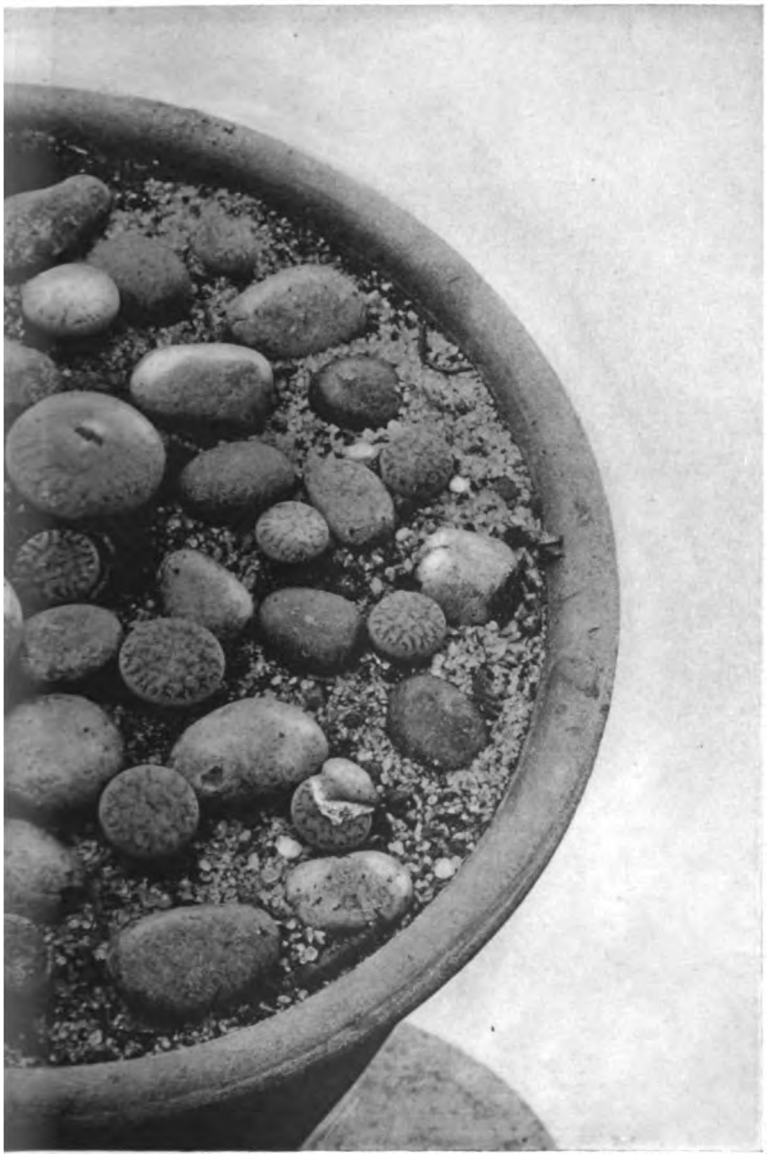
The two preceding plants belong to Ficoideae; the present to the closely related order Portulacaceae. Technically, it is a shrub: the leaves are minute and are concealed by their much larger dry and membranous stipules which form the imbricated investment of the persistent stems. One may wonder what the perplexed palaeontologist would make of the impression of such a plant in the fossil state. It is also a native of the Karru, and Kew is indebted for the specimen shown in the life-size illustration (Plate IX, from a photograph by Mr. E. J. Wallis) to Mr. H. J. Chalwin, Superintendent of the Municipal Gardens, Cape Town, who sent it in 1898. In this case Dr. R. Marloth suggests that the protective resemblance is with 'the quartz pebbles among which it grows.' At the risk of suggesting one perhaps somewhat far-fetched, I must confess that the aspect of the plant always calls to my mind the dejecta of some bird, and the more so owing to the whitening of the branches towards the tips.

My friend, Mr. N. E. Brown, whose unique knowledge of South African plants is the result of the study of a lifetime, tells me that he has long had the plant under cultivation, yet has never succeeded in seeing the flowers. I am indebted to him for the following interesting note:—

'The flowers of *Anacampseros papyracea* are at present unknown to science. I have had the plant under notice for many months, but have never seen a flower. One plant, however, produced several ripe capsules, which were developed at the very tips of the branches, and although I saw the plant daily, the first evidence I had that it had flowered was the protrusion of the young fruit through the dome of papery stipules which

permanently cover the apex of the branches. I therefore believe that the flowers were either cleistogamous or expanded under, and were concealed by the dome of stipules; at any rate they must have been very small. The development of the fruit is rather rapid, and as it matures a short stalk is developed, so that when ripe it is exserted just beyond the apical dome. The capsule is globose, less than ¼ inch in diameter, thin, dry, whitish-brown in colour, and irregularly breaks up into valves, allowing the very small whitish-brown seeds to escape. These are globose and thickly covered with rather long and very fine hairs. I have not yet succeeded in raising seedlings.'

THISELTON-DYER — PRO



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The Structure and Origin of the Cycadaceae.

BY

W. C. WORSDELL.

With seventeen Figures in the Text.

NO family of plants is exciting more interest at the present day than the Cycadaceae, and this for the prime reason that they represent one of those forms of plant-life which link the types of the far past with those of the present modern world. They are placed to-day at the lowest level of the great Gymnosperm-class, but they possess certain peculiarities of habit, external morphology, and anatomical structure which undoubtedly suggest an affinity between them and that large group of the Vascular Cryptogams, the Ferns. The majority of authors who have written on the subject are at one on this broad question of Filicinean relationship. They begin to differ from one another, however, when considering more in detail the group or groups of Fern-like plants to which our modern Cycads are related or from which they have been derived, and also the lines along which the descent with modification has apparently taken place.

The group of Fern-like plants from which our modern Cycads are probably derived is that termed by Potonié the Cycadofilices, but more recently named by Scott and Oliver, Pteridospermeae, itself probably representing a transitional stage of evolution between the Ferns proper and modern Cycads.

Having been asked to contribute a *résumé* of my views as to the origin of Cycads from the Pteridosperms (views which have been founded chiefly on facts of their vascular anatomy), the following account is written in compliance with that request.

The Habit and Structure of Cycads.

I will first give a brief description of the characters of the Cycadaceae.

The Tree-fern-like habit of these plants is the first thing to be remarked; the thick stem often coated externally with an armour-plate of old leaf-bases, bears at its summit a crown of large fronds; but here

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the resemblance in habit to a Fern ceases, unless it be in the Fern-like foliage of the genera *Stangeria* and *Bowenia*. The male and female reproductive organs are borne on cones, each such cone being developed as a direct continuation of the main axis; the growth in length of the plant is subsequently continued by means of a lateral vegetative shoot immediately below the cone, this latter being pushed to one side. The main mode of branching of the plant is thus *sympodial*. But *monopodial* branching also occurs where, as is quite frequently the case, short, lateral shoots are developed at intervals on the main axis. The plants are dioecious. In the case of the female plant of *Cycas* there is no cone developed, the seed-bearing sporophylls arising in groups at intervals directly on the main axis, this latter persisting in growth and developing time after time foliage-leaves above the zone of sporophylls. This is probably a primitive ancestral condition, the cone-formation representing a phylogenetically younger character.

In all Cycads whorls of foliage- and scale-leaves are formed alternately on the vegetative stem.

It would appear that the tap-root of the plant early dies away, its place being taken by adventitious roots which arise from the stem-tissues. This also is a Fern-like character.

All Cycads are xerophytes, i.e. are adapted to withstand the conditions of drought and intense solar heat and light under which they grow; hence the armour-plate of thick leaf-bases on the stem, and the rigidity of structure and thick cuticularization of the leaves.

Let us turn now to the anatomical structure of the vegetative stem. The tissues are extremely parenchymatous and contain an abundance of starch. Mucilage-canals traverse both the wide pith and the cortex, passing also through the medullary rays of the vascular cylinder. They are continuous into the leaf, but not, as a rule, into the root. Periderm is present in the leaf-bases and outer cortex.

Of the nine genera of Cycads, four, viz. *Cycas*, *Encephalartos*, *Macrozamia*, and *Bowenia*, possess more than one vascular ring. In *Cycas* there may be as many as a dozen rings arranged concentrically one within the other. In any case, only the innermost of these rings arises in the first place as primary tissue with secondary cambial formations subsequently increasing its radial thickness. All the other vascular rings are entirely of secondary origin, being formed by the agency of a cambium. The remaining[1] genera, viz. *Stangeria*, *Zamia*, *Ceratozamia*, and *Dioon* possess but a single ring in their stems. Both the xylem and phloem of each are extremely parenchymatous, being largely composed of very numerous medullary rays. This vascular tissue belongs to the collateral type of structure. The leaf-trace bundles, as they enter the stem to the number

[1] But *Microcycas* has never yet been examined.

of two from each leaf, are peculiar from the fact that they describe a girdle-like course part way around the stem, gradually passing inwards to join the central cylinder, having to traverse the medullary rays in order to reach the latter in those cases where two or more cylinders occur. Sometimes, however, as in *Macrozamia*, the leaf-traces pass *directly* inwards.

In all species of the genus *Encephalartos*, and in certain species only of *Macrozamia* there occurs a system of *medullary bundles* scattered in great numbers throughout the pith. Each is always accompanied on the side of the phloem by a mucilage-canal. These bundles are orientated in every conceivable direction as seen in a transverse section, and are collateral in structure. They are cauline in origin, uniting at various points with the primary vascular cylinder, but having no connexion with the leaf-traces.

The roots, both primary and adventitious, vary as regards the number of bundles or rays composing the stele; often the root is pent- or tetrarch at the base, i. e. near the cotyledonary node, becoming successively tri- and diarch as one proceeds towards the apex, but it is often diarch close to the node. A peculiar feature of Cycads is the possession of an apogeotropic root-system; each root branches in a dichotomous coralloid manner above the surface of the soil, and contains in the intercellular spaces of a particular zone of the cortex colonies of *Anaboena*, an Alga belonging to the Cyanophyceae.

The *leaf*, in most genera, is pinnately branched. But in *Bowenia*, *Macrozamia heteromera*, and *Cycas Micholitzii* it is further subdivided. This gives to them a more graceful Fern-like character. This Fern-like character is exhibited by *Stangeria* in another way. Each pinna of the frond possesses a thick midrib containing two or three vascular bundles; the rest of the broad lamina is supplied by dichotomously-branching lateral veins running out to the margin. In *Cycas* the narrow pinna has also a midrib containing a single large bundle, but in this case there are no other bundles in the lamina. The vascular structure of the pinna here is particularly interesting. The bundle of the midrib is of collateral structure with a somewhat arched contour; the xylem is of the mesarch type, i. e. the protoxylem is situated in a more or less central position with, towards the dorsal or phloem side, a little secondary centrifugal, and towards the ventral side a well-developed primary centripetal xylem. Transfusion-tissue, consisting of isodiametric tracheides whose function is to supply with water the mesophyll of the leaf, are situated on either side of the xylem, as seen in transverse section. They really constitute part of the centripetal xylem with which they are connected by elements transitional, not only in space, but also as regards the shape and other characters of the tracheides. The structure of the bundle just described is common to the bundles of the lamina in all genera of Cycads. In *Cycas* the inadequate functions of the transfusion-tissue are

reinforced by an 'accessory transfusion-tissue,' consisting of the central elongated cells of the mesophyll which have become transformed into tracheides, and which extend from the ordinary transfusion-tissue to the margin of the leaf.

In all genera except *Cycas* and *Stangeria* a number of equal, parallel bundles traverses the lamina.

The vascular bundles of the petiole of the leaf are typically arranged in the form of an Ω as seen in transverse section, with the xylems directed inwards or towards the ventral surface of the leaf. There are, however, various complex modifications of this arrangement of which the extreme case is attained in *Encephalartos*, in whose petiole the bundles are extremely numerous, and are orientated in every conceivable direction. The petiolar bundles of Cycads possess the same mesarch structure as those of the lamina, but the centripetal xylem is very great in amount, and is thus strongly contrasted with the very small development of the primary centrifugal xylem.

As regards the vascular anatomy of the cone, the general feature is the possession of a single cylinder of separate bundles, each bundle being collateral in structure with a large amount of secondary superadded to the primary tissue. In certain genera (*Stangeria*, *Bowenia*, *Ceratozamia*) the endarch structure of the bundles at the very base of the peduncle is superseded throughout the rest of the length of that organ by the mesarch character, owing to the presence of scattered primary *centripetal* tracheides, to which is sometimes attached a protoxylem-group distinct from that of the centrifugal part of the xylem.

The sporophylls are spirally arranged on the cone and are short, highly-modified structures, each with a very thick shield-like terminal portion and a narrow stalk. The very numerous male sporangia are scattered in sori over the lower surface of the sporophyll; the female sporangia are two in number, seated likewise on the lower surface of the organ, but on the adaxial side of the peltate portion. Two bundles supply each sporophyll as a rule; these branch so as to form a transverse row of strands. The bundles of the sporophyll which are situated below the level of insertion of the sporangia are characterized by the large amount of centrifugal, as compared with the centripetal, xylem which they possess as a result of their sporangium-supplying function. In the peltate portion of the sporophyll these relations are reversed.

Owing to the fact that they are not compactly grouped together in a cone but are borne loosely on the vegetative axis of the plant the female sporophylls or carpels of *Cycas* are more or less leaf-like in character, and possess rudimentary pinnae in their upper sterile portion. The ovules are usually about six in number (*Cycas Normanbyana* has two), and are borne on the sporophyll in the lateral position of pinnae.

The ovule consists of the following parts: an outer fleshy, often brightly-coloured envelope which is intimately fused with a thick woody shell internal to it, within which again is another soft-celled tissue. The vascular bundles supplying the ovule are divided into two distinct systems: an outer one traversing the external fleshy envelope, and an inner supplying the internal soft tissue.

These, from the purely descriptive point of view, are the main facts of the structure of modern Cycads.

I will now see what we know as to the structure of the *Medulloseae*, a group of the Pteridosperms of which specimens have been obtained from the Coal Measures and the Permian. We know little as to the habit of these plants, but some of the stems found are of considerable thickness and length.

The vascular anatomy of the stem is of great interest, presenting a structure which combines the characters of that of Ferns and modern Cycads, for it exhibits on the one hand polystely and on the other well-developed secondary tissue in each stele.

If we take a species, viz. *Medullosa Solmsii*, which is one of the most Fern-like in its structure, we find, in a transverse section of the stem, a double ring of concentric bundles or steles surrounding a wide pith and surrounded in their turn by a wide cortex. The steles of the inner ring are somewhat smaller than those of the outer. Each individual stele in both rings consists of a central pith, in which primary tracheides are scattered, surrounded by a considerable development of secondary xylem and phloem. Small, concentric leaf-trace bundles occur just outside the outer ring of steles. In the pith are scattered very numerous, minute, concentric bundles, each largely formed of secondary tissue.

In *M. anglica*, Scott, there are only three steles of irregular shape and large size, each possessing a structure identical with that just described. Here and there, immediately outside the steles, is seen a much smaller, isolated, concentric strand termed by Scott 'anomalous' in the sense of representing something extra to the main group of large steles.

The leaf-trace bundles, immediately on leaving the steles, are perfectly concentric in structure, but very soon break up into a small group of collateral bundles, which still further subdivide on entering the leaf.

The stem of *M. porosa*, Cotta, belongs to the type in which the cylinder (at any rate frequently) is composed of a continuous band or zone of vascular tissue, which possesses in itself precisely the structure of one of the concentric steles of *M. anglica*, Scott, or *M. Solmsii*, Schenk. In this species the mutually-inverted parts of the secondary xylem and phloem are respectively equal in development. Numerous medullary bundles, of very much larger size than those of *M. Solmsii*, Schenk, occur, scattered irregularly through the pith; many of them are imperfectly concentric in structure.

M. stellata, Cotta, var. *typica*, exhibits also in the region between the places of insertion of the leaf-trace bundles a continuous zone in transverse section, but here the inner xylem and phloem are very poorly developed as compared with the outer.

M. stellata, Cotta, var. *gigantea*, shows the same character. But here there occur in addition *two or three extra cylinders* from which all traces of the inner xylem and phloem (which may or may not have existed in the ancestor of the plant) are completely absent, so that these zones possess a collateral structure. They appear also to be entirely secondary in origin, for there are no signs of primary tracheides.

In *M. Leuckarti*, Göpp. and Stenz., there is a main cylinder composed of two or three very irregular, sinuous, elongated steles of considerable development; within this is a minor cylinder of similarly-shaped, but smaller steles, which abstricts off at places the smaller steles which compose the medullary system.

In *M. porosa*, Cotta, and *M. Solmsii*, Schenk, there is likewise an inner minor cylinder, but composed, in the first-named species, as also in *M. Solmsii*, Schenk, vars. *incrassata* and *lignosa*, of steles greatly reduced in size as compared with the main cylinder, forming in this respect a transition to the medullary steles lying irregularly scattered in the centre. They exhibit, moreover, the peculiarity of having the secondary xylem and phloem developed on the *inner* side only, and are therefore collateral in structure.

The foliage now known to have been borne by Medullosean-stems was that known as *Alethopteris* and *Neuropteris*[1], the characters of which are very Fern-like.

The petioles of these fronds, known as *Myeloxylon*, possess, as seen in transverse section, an outer cortical region exhibiting the 'Dictyoxylon' sclerotic tissue; the rest of the organ contains large numbers of collateral, usually exarch bundles, orientated in every conceivable direction.

We will now describe the main features of the anatomy of another type of the Pteridosperms, viz. *Lyginodendron*. A transverse section of the *stem* of *L. Oldhamium* reveals the following structure: an outer 'Dictyoxylon' cortex; an inner soft-celled cortex; a periderm, probably arising from the pericycle; a central cylinder composed (frequently) of a number of more or less distinct and separate bundles each of which possesses the following structure: a mesarch primary xylem-strand, consisting of a central protoxylem with, on the inner side, a well-developed centripetal, and, on the outer side, a small amount of centrifugal xylem; attached to the outer side of each such primary strand is a thick fan-shaped mass of secondary xylem, bounded on its external side by a very much less-developed zone of phloem. Opposite each gap between the bundles a single large leaf-trace,

[1] Probably also other types, such as *Odontopteris* and *Linopteris*, belonged to them.

possessing a thick arc-shaped mass of secondary xylem, passes off; it soon divides into a pair of strands within the pericycle: these lose their secondary tissues, and, on passing into the leaf, again fuse into a single strand. Certain abnormal structures in the cylinder were also observed. Occasionally a cambium (which, in some cases, may form a continuous arc stretching from the normal cambium of one side of the bundle, round the inner side of the centripetal xylem, and joining the normal cambium of the opposite side) arises on the inner (ventral) side of the primary strand, there forming xylem and phloem with inverted orientation. Sometimes this abnormal cambium forms parenchymatous tissue only.

The foliage borne by *Lyginodendron*-stems was that termed, before its real relationships were established, *Sphenopteris Hoeninghausii*; it was very Fern-like, with finely subdivided segments. The petioles bearing these laminae bore the name of *Rachiopteris aspera*. A transverse section of this latter revealed a single large bundle of mesarch structure, with three or more protoxylem-groups situated near the periphery of the xylem; the whole was completely surrounded by phloem. The outer part of the cortex exhibited a Dictyoxylon-structure.

In *Heterangium* there is a single large solid stele in the stem, the structure of which is precisely that of one of the separate steles of the stem of *Medullosa anglica*, &c., but the whole is on a larger scale. The characters of the cortex, leaf-traces, and petiolar bundles are similar to those in *Lyginodendron*. The foliage belonging to the stem is that known as *Sphenopteris elegans*.

The Origin of Cycadean Structures.

1. *Origin of Axial Structures.*

Most botanists are agreed that modern Cycads had their origin somewhere in the plexus of the Carboniferous or Permian Pteridosperms (Cycadofilices). If this is the case some indication of that origin should be discovered in the anatomical structure of the caulome or shoot. But opinion is divided as to which of the Pteridospermic types of stem-structure that of modern Cycads has been derived from. There is, on the one hand, the view which regards the central cylinder of the Cycad as derived from that of *Lyginodendron* or *Heterangium*, while the 'extrafascicular' cylinders of certain Cycads are held to be peculiar to them and of no ulterior phylogenetic importance or value. On the other hand, there is the view which regards the Cycadean cylinder as derived from that of such a form as *Medullosa porosa*. This latter is the view I shall adopt in this paper.

Now, in the first place, I will start out with the primary proposition that if ancestral characters are present at all in the vascular tissue they must be

sought for in two principal regions, viz. (1) in the *cotyledonary* or *primary node*, i.e. the approximately transitional region between root and stem; for it is here that the *earliest* tissues of the vascular system arise, and we know that it is in these tissues, developed earliest in the ontogeny, that ancestral traits are most likely to be found and recognized; (2) the *flowering axis*, for in this region the vascular tissue will have undergone *less modification*, than is the case with the vegetative stem, in the direction of subserving the

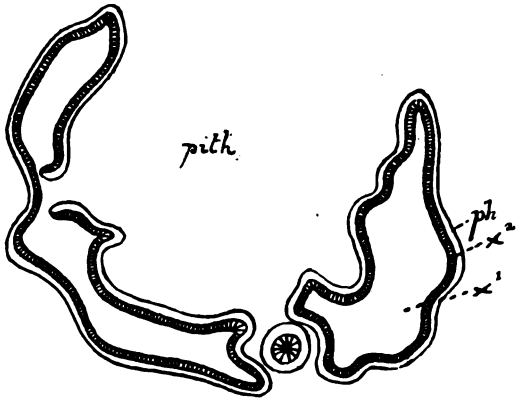

FIG. 1.

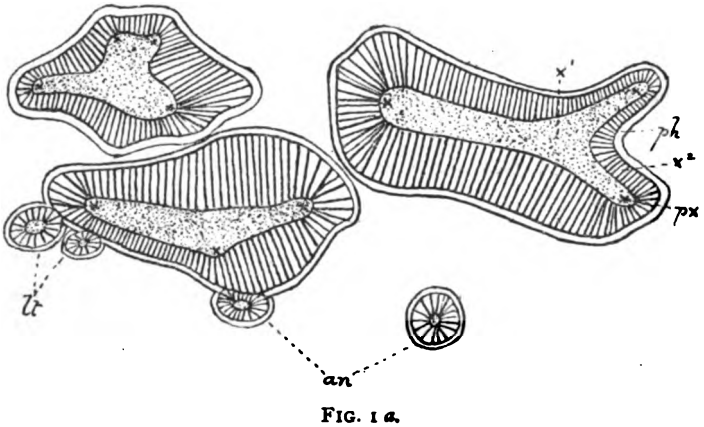

FIG. 1 *a*.

FIG. 1. *Encephalartos Barteri*: diagrammatic transverse section of the seedling-axis in the region of the cotyledonary node, showing the medullosa-like steles (after Matte). FIG. 1 *a*. *Medullosa anglica*: diagrammatic transverse sections of vascular system of stem, showing three main steles, two accessory steles, and two leaf-traces (after Scott): *ph* = phloem; *px* = protoxylem; x^1 = central primary xylem; x^2 = secondary xylem.

exigencies of conduction, and hence ancient characters which may be present will tend to be less obscured by the later adaptive accretions to the structure.

If, then, we examine the cotyledonary node of the stem of certain Cycads we find structural phenomena which, in my opinion, shed great light on the origin of the vascular tissue of the axis as a whole.

Matte found in this region of the stem of a seedling of *Encephalartos Barteri* (as viewed in transverse section), instead of the usual continuous cylinder of endarch structure, *three* practically *independent, distinct steles*, each of very sinuous, irregular contour, and not forming a definite cylinder (Fig. 1). This is, to my mind, the most important recent discovery in the structure of Cycads. Its significance, for my point of view, is immense. For this structure is clearly exactly comparable to that of such a type as *Medullosa anglica*, Scott (Fig. 1 *a*), above described[1]. It is an ancestral character, found here, and here only, in the very region we should most expect it, and soon lost as, passing upwards, the steles unroll and gradually

FIG. 2. *Stangeria paradoxa*: transverse section of lower (not lowest) region of vascular ring of peduncle of cone showing irregular orientation of the bundles (diagrammatic and reversed) (after Scott).

constitute the typical cylinder. This is the only instance of the kind hitherto observed in the vegetative stem.

In the structure of the peduncle of *Stangeria*, however, there is, in my opinion, further evidence available that the central cylinder is in reality composed of the one-sided remnants of a number of steles. In the *lowest* part of the peduncle there is nothing exceptional to be seen; but somewhat higher up, i.e. sufficiently so for the organ to exhibit its distinctive character, uninfluenced by the region of its origin lower down, the component bundles of the cylinder become orientated in a very irregular way: some lying back to back, with their long axes directed towards the centre of the organ, and at the same time more or less incurved at the ends, while others are horse-shoe-shaped; and one is completely *concentric*, with central protoxylem (Fig. 2). This peculiar structure can be readily explained if we suppose that the whole cylinder has been derived by

[1] Dr. Matte informs me that there was no trace of any injury to the tissues in this region of the seedling-axis. He observed this structure in a single individual only; other seedlings did not possess it. He has since kindly enabled me to examine the sections for myself.

fragmentation of a few (two or three) steles of extremely *sinuous* contour, such as are found in the stem of *Medullosa Leuckarti*, Göpp. and Stenz. (Fig. 3). If all the bundles, instead of only one or two, resulting from this fragmentation had remained concentric, we should have a structure like

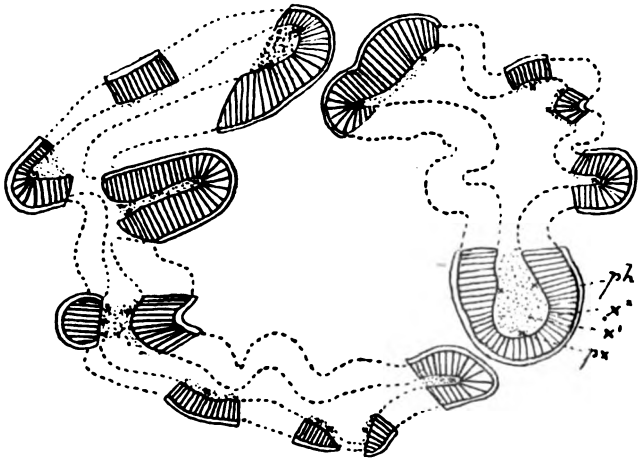

FIG. 3. *Medullosa Leuckarti*: transverse section of vascular system of stem, schematically drawn to represent how the vascular structure of *Stangeria* (illustrated above) could have been derived by fragmentation of the large irregularly shaped steles, the dotted outlines representing the eliminated portions.

that of *M. Solmsii* (Fig. 4), whose polystelic character I regard as probably derived from the solenostelic condition of such a form as *M. porosa*; on this view the structure of *M. Leuckarti* would represent a kind of intermediate stage between the two.

The incurved and horse-shoe-shaped bundles of *Stangeria*, I am convinced, possess a great phylogenetic and morphological significance: they are the remains of the concentric bundles or steles of the Medullosean ancestor. This easy explanation of the phenomenon seems to me the *only* one possible. It is only in this lower region of the peduncle that this ancestral trait can maintain itself; higher up the bundles become orientated in the normal manner in order to adapt themselves to the modern economic necessities of conduction. Higher up also, the *centripetal xylem* appears more in evidence; this too, with Scott, I regard as an ancestral character, as its tardy appearance in the ontogeny would help to indicate. In the concentric and horse-shoe-shaped bundles of the lower region it is absent, the available space for such a tissue

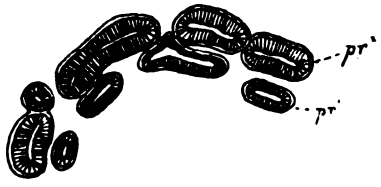

FIG. 4. *Medullosa Solmsii*: transverse section of part of double vascular ring of stem; pr^1 = inner primary ring; pr^2 = outer primary ring (reversed and in part restored) (after Weber and Sterzel).

in the interior of those strands being reduced to a minimum. I regard these primary centripetal tracheides (whose rudimentary nature is further betrayed by the half-hearted way in which they assume the stain) as of probably dual origin: I hold that for the most part they represent the central primary tracheides of the stele of *M. anglica*; in this case we must imagine the protoxylem, centrifugal xylem and phloem of that part of the stele nearest the pith of the peduncle to have completely died away. Occasionally, however, these three tissues are present on the inner side of the bundle, while, in the wide area between them and the normal bundle, numerous 'centripetal' tracheides are seen. In such a case these inner tissues are well developed and not rudimentary in appearance; they merely represent an incurved portion of a horse-shoe-shaped stele which has become detached and independent (Fig. 5). Such a strand sometimes anastomoses with the *ventral* portion of the bundle to which it is opposite. In other cases, however, a group of centripetal tracheides is united, on its pith-side, to an extremely rudimentary phloem-strand, or this latter may be replaced by a rudimentary cambium. It seems possible, therefore, that in some cases the 'centripetal xylem' may represent the vestiges of the *centrifugal* xylem (primary or secondary) of the ventral part of the original and primitive stele, the protoxylem belonging to which has become extinct.

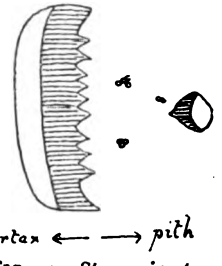

FIG. 5. *Stangeria paradoxa*: transverse section of a single bundle from vascular ring of peduncle, showing small strand on inner or pith-side of large strand, with groups of centripetal tracheides lying between the two (diagrammatic).

As regards the mode of *ontogenetic* origin of all or any of these structures, it has probably not the remotest connexion with their *phylogenetic* history. The chief point about this remarkable structure has hitherto been, apparently, missed.

Scott, however, lays great stress on his belief that the 'centripetal' xylem, as found in the peduncle of *Stangeria*, *Bowenia*, and *Ceratozamia*, is the homologue and derivative of the centripetal primary xylem occurring in the bundles of the vegetative stem of *Lyginodendron*, *Heterangium*, *Poroxylon*, *Calamopitys*, &c. In this we entirely concur. But we differ as to the mode of origin of the vascular tissue in these fossil plants. Scott regards the solid monostele of the *Heterangium*-type as the primitive form in this group; the *Lyginodendron*-type he holds to be derivative therefrom. According to his view the centripetal xylem of *Lyginodendron* represents the last peripheral remnant of the great mass of primary xylem which, along with parenchyma, occupies the entire internal area of the *Heterangium*-stele. My view, on the contrary, embodies the belief that *each* primary xylem-group in *Lyginodendron*, along with its mass of secondary centrifugal xylem and phloem, is the one-sided remnant of an *entire stele*

or *concentric bundle*, and is hence precisely comparable to, and homologous with, each bundle in the peduncle of *Stangeria*, &c.; both, in my opinion, have been derived phylogenetically from a single stele, like one of those composing the cylinder of *Medullosa*. The following are my reasons for holding this isolated position. In many stems of *Lyginodendron* the bundles are more or less separate from one another, or in groups of two, due to lateral anastomosis; each single or double group of primary xylem having an *arc- or fan-shaped* mass of secondary xylem attached to it (Fig. 6); this in itself is an indication of the stelar origin of the bundle; otherwise, how is this arc-like character to be explained?

The fact that arc-shaped leaf-trace bundles are cut off from the cylinder (which may occasionally be concentric, thus resembling the case of *Medullosa*) will not explain the phenomenon; for similar arc-shaped leaf-traces pass off from the stele of *Heterangium*; the arc-shaped character is one which is inherent in the stem-bundles as such.

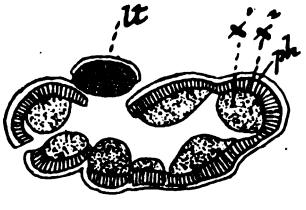

FIG. 6.

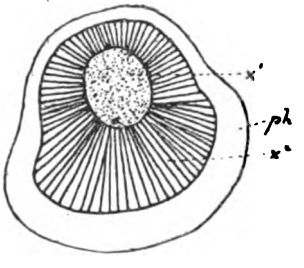

FIG 7.

FIG. 6. *Lyginodendron Oldhamium*: transverse section of vascular ring of stem of young plant, lt = leaf-trace (diagrammatic) (after Williamson and Scott). FIG. 7. Transverse section of single bundle from vascular ring of stem, showing its concentric stele-like structure, the remaining bundles of ring had same structure (from slide no. 1138 of Williamson Collection in British Museum) (diagrammatic).

In some stems, however, where the bundles are more isolated, the cambium of the dorsal side extends right round the centripetal xylem on the ventral side (Fig. 7), though its secondary products in this region, as might be expected, are much less in amount, the parenchymatous often outnumbering the xylem-elements. This phenomenon strongly supports my position as to the *polystelic* origin of the *Lyginodendron*-cylinder. Scott, on the other hand, maintains that they do not in the least disturb *his* position as to the *monostelic* origin of the latter; for these extra tissues, giving rise to the concentric structure, are purely *secondary*, formed by a cambium which, in his opinion, may appear on the scene *at any time and under any circumstances*, and to which, therefore, no morphological significance is to be attached. He regards it as the same anomaly as occurs in *Acanthophyllum* (Caryophyllaceae), in *Iodes tomentella* (Olacineae), and in *Tecoma* (Bignoniaceae), and as far as the bare facts are concerned, these latter cases are, doubtless, comparable with that of

Lyginodendron. In the case of *Lyginodendron*, the *near allies* of the plant, viz. *Cycadoxylon*[1] and Medulloseae, exhibit this 'anomaly' as the *normal* structure in their stem. Hence, the comparative method of investigation strongly supports my hypothesis that this so-called 'anomaly' in *Lyginodendron* is a *reversion to an ancestral character* whose appearance is rendered possible by the late formation of interfascicular cambium in the stem. The isolated, sporadic, and (often) rudimentary characters of this 'anomaly' support my view; for these are precisely the features which distinguish ancestral structures wherever they appear.

I should, therefore, regard each bundle of the normal stem of *Lyginodendron* as itself the equivalent of a single complete stele in the stem of *Medullosa anglica*, of which the protoxylem, primary centrifugal, and secondary tissue belonging to the ventral or pith-side of the stele have completely vanished. I admit the bare possibility of what I cannot help regarding as a quite meaningless cambium appearing on the scene; but this mechanical view of the matter I regard, in the light of the facts cited above, with very much less favour than the one already given. Moreover, Scott, so it seems to me, is inclined to attach a far too great significance to the difference existing between primary and secondary tissues. In my opinion there is no *essential* difference between primary meristem and cambium, the difference merely lying in the *varying periods* at which they respectively arise, each having, in accordance therewith, its own peculiar characteristics. And the secondary tissue is one of the great and characteristic features of the group of plants with which we are dealing.

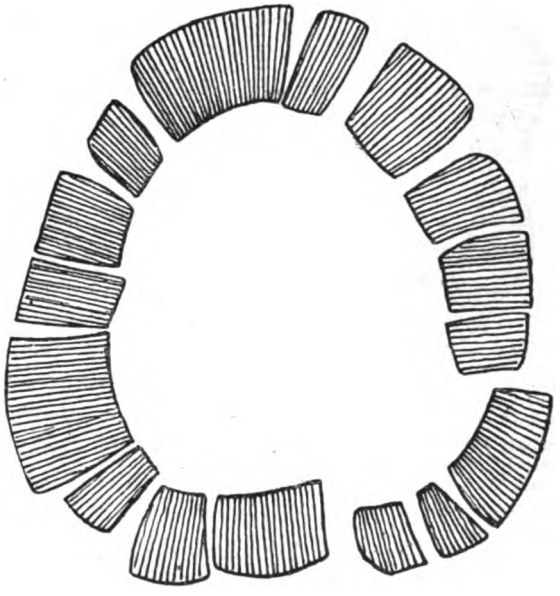

FIG. 8. *Heterangium Grievii*: transverse section of secondary wood of stele of stem, showing entire absence of any curvatures save those which are necessary for maintaining the cylindrical contour of the stele as a whole (diagrammatic).

Owing to the *even, uncurved contour* of its ring of secondary xylem (Fig. 8) (so contrasted with that of the ring of secondary xylem in *Lygino-*

[1] Cf. Seward's '*Lyginodendron robustum*.'

dendron, in which the *sinuous*[1] character can always be more or less clearly traced, Fig. 9), and the character of the entire general structure, I regard the single large monostele of *Heterangium* and, I would add, of *Megaloxylon*, as equivalent to a *single stele* of *Medullosa*. The very sinuous contour of many Medullosean steles is due to two causes: firstly, to the perpetual anastomoses occurring between neighbouring steles, and secondly, to the constant abstriction of concentric leaf-trace and medullary bundles; but these two causes will not account for the sinuosity of the central cylinder of *Lyginodendron*. There may be traced a gradual reduction in the number of steles composing the cylinder: (1) the very numerous ones of *M. Solmsii*; (2) the three or four *much larger* steles of *M. anglica* or *M. Leuckarti*; (3) the *single* stele of *Heterangium* and *Megaloxylon* which, owing to space-relations, is naturally and inevitably of much greater dimensions than, while preserving an identity of structure with, the steles of other members of the group. Hence, on my view, *each individual bundle* and not, as Scott holds, the entire cylinder, of *Lyginodendron*, is the homologue of the large stele of *Heterangium*, &c.[2]

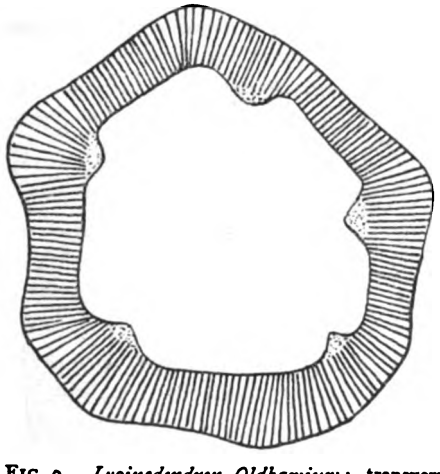

FIG. 9. *Lyginodendron Oldhamium*: transverse section of secondary wood of stele of stem, with primary xylem-groups included, showing bulging of the ring opposite the primary bundles, due to other causes than the natural curvature of the cylinder (diagrammatic).

At the *bases* of branches of *Lyginodendron*, as described by both Williamson and Lomax, the primary centripetal xylem-groups *tend* to become continuous (although complete continuity never obtains), while the

[1] Cf. Williamson's Figs. 1, 2, 4 (Plate XXII), and 6, 7 (Plate XXIII), of *Lyginodendron* with his Fig. 30 (Plate XXVIII) of *Heterangium* (Organ. Fossil Plants of Coal-Meas., Part iv, 1873). Also Williamson and Scott's Fig. 1 (Plate XXI) and their Photo. 1 (Plate XVIII) of *Lyginodendron* in their joint paper of 1896 with Williamson's Fig. 1 (Plate XXI) in his memoir of 1887. Williamson's Fig. 2 (Plate XXII) of the same memoir, showing part of the transverse section of the stem of *Heterangium tiliaeoides*, shows a somewhat sinuous contour of the ring, but it will be noted that even here the secondary xylem is never arched around each primary xylem-group as it always is in the case of *Lyginodendron*. Whenever a section of the *entire* cylinder is seen this striking fact becomes incontrovertible.

[2] Any argument for the close affinity of *Lyginodendron* and *Heterangium* drawn from the fact that they both bore a Sphenopteroid type of foliage can have little weight in view of the fact that several forms of *Sphenopteris*-foliage belonged to the true Ferns bearing such fructifications as those named *Renaultia, Discopteris, Dactylotheca, Oligocarpia*.

Again, the stem of some species of *Davallia* is polystelic, that of other species is solenostelic, yet the same type of foliage obtains throughout the genus. It is not, therefore, very strange to find a considerable latitude in the character of the stelar anatomy of Pteridosperms bearing *Sphenopteris*-foliage.

pith becomes much smaller in diameter, the centripetal xylem occupying an important part of the area enclosed by the secondary wood. The latter tissue at the same level forms a continuous, compact ring in which the sinuous character is very much less evident than is the case at a higher level of the branch. The result of all this is a much greater resemblance of the structure of the branch-base to that of the mature stem of *Heterangium* than is the case with the structure at a higher level of the branch where the *typical Lyginodendron*-features reappear.

I do not regard this as having any phylogenetic significance, for the ontogeny of the structure of a shoot need not necessarily repeat its phylogenetic history. The explanation appears rather to be a mechanical one: the concentration, both in a radial and tangential direction, of the woody vascular tissues is probably an adaptation for the resistance of tension and bending-strains to which the shoot-base must become subject. The same adaptation may be observed in Ferns, as in the base of the stem of *Osmunda*, of the branches of *Blechnum Spicant*, and others. It occurs at the base of the stems and branches of Dicotyledons. In the base of the peduncle of *Stangeria* the centrifugal xylem of the ring becomes congested in this way, and it is only at a higher level, where the *typical* structure of the organ is assumed, that ancestral characters, such as the presence of the centripetal xylem, begin to appear, thus proving that the structure prevailing at the base of the organ is purely adaptational in character and of no phylogenetic significance. *It is to the typical mature structure, and not to the early stages of its ontogeny, that we must look for the occurrence of ancestral characters.* The subject cannot be entered upon now, but might well repay further investigation. I believe myself that, in all likelihood, far too much has been made of the idea that the successive anatomical structures exhibited in the ontogenetic history of Ferns and other plants is a repetition *in parvo* of similar structures developed during the course of the phylogenetic history.

Further evidence in support of the view set forth above as to the origin of the *Lyginodendron*-structure is afforded by the early occurrence—viz. in the Calciferous Sandstone—of that polystelic member of the same group we are considering, *Cladoxylon*. I may add, as a final corollary to this part of the subject, an opinion which I have elsewhere expressed: 'that the derivation of the tubular from the solid stele is to be sought for, not in these semi-gymnospermous forms, but much farther back, viz. among the Ferns!'

In *Med. Solmsii* and *M. Leuckarti* (some forms) the two primary rings of steles differ in that the steles of the innermost ring are smaller and less developed than those of the outer. In *M. porosa* there is also an inner ring which may be said to be formed by the *regular annular grouping* of certain of the small medullary steles. In fact, transitions exist between

the medullary system and the inner cylindrical system of steles. I hold, further, that in the Medulloseae the cylindrical and medullary systems are merely *variants of a single system.* That the annular or cylindrical system has either been derived in the past from a primitive system of irregularly scattered steles, of which the medullary strands are the surviving remnant; or, on the other hand, that the cylindrical system is primitive, and has itself given origin to the medullary system. I am inclined to regard the latter as the most probable view.

In most cases the medullary steles are perfectly concentric in structure, but this is not always so; e.g. in *M. porosa* the outermost, as also several of the more central, steles are imperfectly concentric; in such cases the resultant collateral or sub-concentric stele is very variously orientated, according as the secondary tissue is defective on this or that side of it.

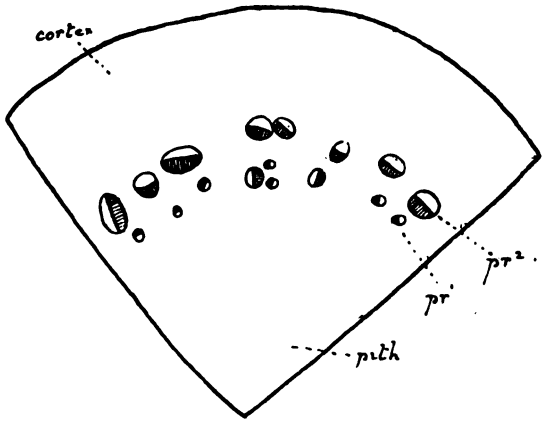

FIG. 10. *Ceratozamia latifolia*: transverse section of part of vascular system of fertile region of cone-axis, showing inner primary ring of small bundles (diagrammatic).

Now in the modern genera *Encephalartos* and some species of *Macrozamia* there is a medullary system of, usually, very small and very numerous *collateral* bundles of extremely various and irregular orientation; this latter may be primarily due to the causes just mentioned in the case of *Medullosa*; but appears more directly traceable to the fact that each bundle follows the sinuous course of a mucilage-duct towards which its phloem is always orientated. But the cauline origin of these medullary bundles may be attributed to the fact that they constitute one and the same system with those of the vascular rings.

In the fertile part of the axis of the male cones of *Ceratozamia mexicana*, Brongn., and *C. latifolia*, Miq., I observed the rudiment of an *intrafascicular* primary cylinder of bundles; these latter were much less developed than those of the outer cylinder; they were in one of the species arranged frequently in small groups of three (Fig. 10), representing small fragmented concentric structures, for their xylems were mutually orientated towards each other; other isolated bundles were inversely orientated; in the other species the inner bundles were much less numerous and usually rudimentary in development, staining badly; one such was observed to be perfectly concentric in structure and to end blindly upwards. In both

cases I regard these inner bundles as an ancestral remnant of the innermost cylinder of primary bundles above described in certain Medulloseae. The same will hold good for the two primary cylinders in the peduncle of the cone in *Encephalartos*, of which the outermost, divided up into irregularly formed groups of *concentrically-arranged* bundles, supplies the sporophyll-traces. Matte gives beautiful illustrations of this pleiocylindric character in the peduncle of the cone of *Encephalartos villosus* (Fig. 11).

The inversely orientated strands occasionally occurring on the *dorsal* side of the bundles of the normal cylinder or arc of the peduncles and sporophylls respectively, receive also their explanation from a study of Medullosean anatomy. This phenomenon is due to the presence in that position of a stele, or the rudiments of such, which, instead of, as in the case of the usual bundles of the cylinder or arc, lacking the ventral portion of the primitive stele, exhibit a complete abortion of the *dorsal* half thereof. But in one or two cases, signs of slight cambial activity on the outer side of such strands indicate an attempt at reversion to the primitive state of things. Frequently these strands are continuous with those of the normal cylinder by means of an involution of their tissues; this is also the same phenomenon as was described by Gregg in the root of *Cycas Seemanni*; in that case, however, the outer half of the usually incomplete stele is present, and is continuous as an independent continuous zone right round the entire root-stele.

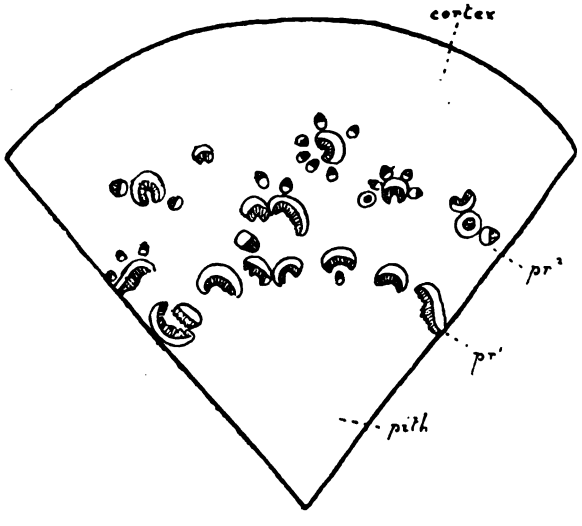

FIG. 11. *Encephalartos villosus*: transverse section of part of vascular system of peduncle of cone, showing outer primary ring consisting of groups of bundles (after Matte) (diagrammatic).

In the case of the cone the inversely orientated dorsal strands are *primary*; hence we here see another instance of the presence of two primary cylinders (or parts of such) like those already described. As a comparison with what I found in the case of *Encephalartos*, we may note that Scott says, speaking of *Ceratozamia*: 'some of these [inverted cortical] bundles, where they pass further out into the cortex, show some

approximation to a concentric structure[1].' Here we see clearly preserved in the cone-axis traces of a *second cylinder*. This latter has long since disappeared from the *vegetative* axis, *Ceratozamia* being one of the *monocylindric* forms.

Let me now pass to the consideration of the 'extrafascicular' secondary strands and zones; they occur, as mentioned above, in the stem of four genera of modern Cycads, and in that of *Medullosa stellata*, var. *gigantea*. The structure of this latter is almost exactly a replica of that of a modern Cycad which possesses it. I will therefore consider them together. At the outset I may say that I regard *all* the cylinders or rings as mutually *homologous*, and that there exists no morphological distinction between the primary and secondary zones. The comparatively late period at which all vascular rings except the first arise necessitates their earliest beginnings being inaugurated by a *cambium*; but this does not render them in any way different in nature from the first-formed one. What is, therefore, the origin (which must be the same for all) of these zones?

In certain Medulloseae, as in *M. stellata*, var. *lignosa*, *M. Solmsii*, vars. *incrassata* and *lignosa*, the *outer* part of the secondary wood of the *primary* cylinder has far exceeded in thickness that of the *innermost* portion which has become, as it were, left behind on the road of advancement. In explanation of this phenomenon I may quote my own words of nine years ago[2]: 'as time went on, and greater specialization in the conducting-tissues arose, and a need for the formation of a larger amount of this tissue became urgent, the cambium of the inner portion of each such concentric strand gradually became less and less functional, that of the outer portion, on the contrary, more and more active, so that a much larger quantity of wood and bast became formed on the outer side of each strand than on the inner side, for this was the surest and best means of economizing both space and expenditure in the building up of an efficient conducting-tissue for the stem.'

The primitive condition, in which the secondary wood was of equal development all round or on both sides, is seen in the polystelic cylinder of *M. Solmsii* (Fig. 4), and in the solenostelic cylinder of *M. porosa* respectively.

In the case of the Medulloseae the innermost part of the secondary wood of the primary ring, never, as far as we know, became extinct; in modern Cycads, on the contrary, it became, along with the phloem (except in the case of *Encephalartos Barteri*, described above), completely extinct.

As regards the *outer secondary rings*, it is a remarkable fact that these, in the stem of *Med. stellata*, var. *gigantea*, had, apparently, already com-

[1] Matte describes the same phenomenon in the peduncle of *Bowenia* and *Ceratozamia*. In the latter he also figures *concentric* and arc-shaped bundles in this position.

[2] Dec. 1896.

pletely lost their inner inverted secondary tissues; this is, possibly, also the case with *M. Solmsii*, var. *lignosa*. That the primitive type possessed two or more *solenosteles* of *secondary* origin we do not know. It is possible that these outer secondary zones may have been collateral in structure from the beginning, but this, in the light of the structures presently to be described in some Cycads, is not probable; yet even if it were so, these zones would still have to be regarded as morphologically equivalent to the *outer or dorsal half* of a solenostele, and, therefore, these 'extrafascicular' collateral cylinders are morphologically *derived from solenosteles*, owing to the fact that the *primary* ring possesses the structure of this latter; and all the rings are to be regarded as homologous.

Let us consider now the case of the Cycadaceae. In that most primitive part of the axis of the plant (see *supra*), viz. the *cotyledonary node*, Gregg (in *Cycas Seemanni*), I myself (in *C. revoluta*, *Encephalartos horridus*, *Macrozamia Denisonii*, *Bowenia spectabilis*), and Matte (in *Cycas siamensis*), observed and described a *polystelic* structure controlling either the whole or part of the first-formed *secondary* cylinder, i.e. the first 'extrafascicular' ring. Immediately outside the very sinuous contour of the root-stele Matte figures a number of concentric structures or steles, some of which are in the act of separating off from the central stele (Fig. 12); this will, perhaps, account for the imperfect continuity of contour of some of the steles. As in the cases of *Cycas revoluta* and *Bowenia* observed by me, some of the steles have a thicker layer of secondary wood on their *inner* than on their outer side. This ancestral stelar structure, wherever it occurs, becomes replaced, *higher up* in the axis, where modern tendencies hold supreme sway, by a *continuous*, *collaterally-constructed* cylinder; if traced downwards into the root these steles merge into the central cylinder. In the mature plant all trace of these structures in the cotyledonary node would probably be lost.

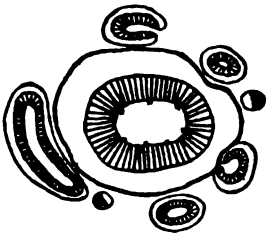

FIG. 12. *Cycas siamensis*: transverse section of vascular system of seedling-axis in region of cotyledonary node, showing outer ring of steles (diagrammatic and reversed) (after Matte).

In *Encephalartos horridus* I observed 'on the dorsal side of, and closely abutting on the large [concentric] strand [of the first "extrafascicular" cylinder] . . . two other smaller ones of the ordinary collateral structure and orientation. At another level two strands are seen, one on each side of the large one, each with a considerable amount of secondary thickening, one of which has *inverted orientation*.' 'Further out in the cortex are scattered other much smaller bundles with inverted orientation. Another group of three bundles was observed, *with their xylems mutually directed towards each other*.' These smaller strands I regard as the first sporadic

beginnings of the second, third, and fourth 'extrafascicular' cylinders respectively; it will be noted that two of them exhibit traces of the primitive concentric or stelic structure.

In the basal region of a mature stem of *Macrozamia Fraseri* I observed small, rudimentary *inverted* strands on the inner side of the first and second 'extrafascicular' rings; these, doubtless, represent the corresponding portion of the *concentric* strands which were seen to occur immediately outside the central cylinder in the same region of the stem in a young plant of *M. Denisonii*; they are very interesting as showing how such ancestral and (for modern requirements) unnecessary parts of the structure become swamped and rendered utterly obscure as individual growth proceeds.

In the same region of the stem of *Cycas Seemanni* I found the first 'extrafascicular' ring to be composed of *concentric* strands situated at wide tangential distances apart, which differed from those composing the corresponding ring in *Macrozamia* and *Encephalartos* in having a symmetrical contour, the tissues being of the same thickness all round; the ring next outside this formed a continuous zone having a collateral structure. In the same region of the axis of another individual but at a slightly lower level, viz. where root-structure of the central cylinder occurred, the first 'extrafascicular' ring consisted of a much broken-up collateral zone; one or two of the isolated strands possessed an almost equal amount of *inverted* xylem and phloem on the *inner* side. The second extrafascicular ring is a continuous thick collateral zone with, at intervals, some extremely *minute*, *rudimentary*, *inverted* bundles on its inner side; these represent the last faint traces of the former solenostelic structure of this ring. The third ring exhibited much the same characters as the first.

In all species of *Cycas* the stem possesses throughout its length a *cortical* system of perfectly *concentric* secondary strands which are *cauline*, terminating above in the base of a leaf and connected, during their course, with incoming leaf-traces. They appear to be peculiar to the genus *Cycas*, and to have no exact counterpart in the Pteridosperms. In any case, they are interesting; for they constitute an outlier from the main conducting-system of the stem, and hence have escaped all those modern influences which have reduced the ancestral concentric structure of the main rings for the most part to the collateral type. This outlying ring of concentric strands resembles precisely the first 'extrafascicular' ring of strands observed by me in the case of the stem of *C. Seemanni*, and also the 'accessory vascular strands' described by Scott in the stem of *Med. anglica*. In all these cases the central, irregularly-scattered tracheides, which so greatly resemble *primary* elements, are in reality the first-formed *secondary* tracheides of the wood of the stele. The same isodiametric elements can be found on the inner side of the 'extrafascicular' collateral rings in all Cycads which possess them.

There thus appears a mass of clear and conspicuous evidence in favour of the derivation of both the primary and the secondary endarch rings or cylinders of Cycadean stem-organs, from the poly- or solenostelic structure of the same organs in the Medulloseae. The hypothesis of the appearance on the scene of a *meaningless* cambium in order to account for the inverted ventral strands, I find myself quite unable to accept.

2. *Origin of Foliar Structures.*

The Fern-like character of the foliage of the Pteridosperms we found to be still represented in that of certain of our modern Cycads. We should therefore expect to find in the anatomy of the foliar organs of Cycads further indications of their Pteridospermic ancestry.

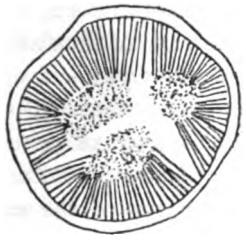

FIG. 13.

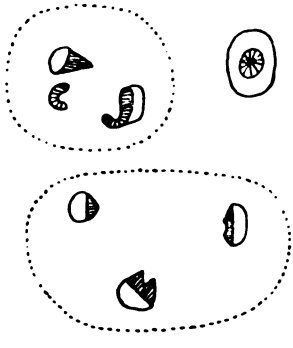

FIG. 14.

FIG. 13. *Medullosa stellata*: transverse section of leaf-trace bundle just after leaving central cylinder, showing the three component parts into which it eventually splits (diagrammatic and partially restored) (after Weber and Sterzel). FIG. 14. *Stangeria paradoxa*: transverse section of three sets of leaf-traces, two of which are broken up into their constituent strands, the other being entire (diagrammatic).

Firstly, I may refer to the structure of the vascular bundles. In *Medullosa* the leaf-trace bundles on leaving the central cylinder of the stem are perfectly concentric (Fig. 13), but shortly each breaks up into a number of collateral strands. In *Lyginodendron* and *Heterangium* the bundle only assumes the concentric structure after entering the leaf, where refusion of the two, which were the result of division of the leaf-trace in the pericycle, takes place. But in certain stems of *Lyginodendron* some of the leaf-trace bundles were perfectly *concentric* in structure.

Now I observed in the peduncle of the female cone of *Stangeria* that some of the sporophyll-traces immediately on leaving the central cylinder appeared in the form of three separate small bundles grouped around a common centre, so that such a group may be said to represent, as it were, a *fragmented concentric bundle.* Further out in the cortex these bundles became completely separated from each other. In the

outer part of the cortex one or two of the bundles supplying the *barren sporophylls* possessed three distinct groups of *xylem*; this is probably a relic of a similar tripartite bundle as that above described and as is also found in *Medullosa*. Quite frequently a perfectly *concentric* sporophyll-trace occurs in the neighbourhood of other collateral traces and too far out in the cortex to belong to the cauline system of strands (Fig. 14). Here, then, we see some last obscure remnants of the ancestral leaf-trace bundles in precisely that part of the plant where we should most expect to find them.

In Cycads the leaf-traces leave the cylinder, as a rule, in groups of two [1]; in the peduncle of *Encephalartos villosus* Matte observed groups of three to five leaf-trace bundles passing out. The bundles have very often their xylems *slightly directed towards each other*. Each group of one, two, or more may be regarded as the equivalent of the single concentric leaf-trace of *Medullosa*; in the case of Cycads fragmentation and reduction of the leaf-trace has taken place *congenitally* (i. e. *before* the trace left the cylinder); in the case of *Medullosa* it has occurred *postgenitally* (i. e. *since* leaving the cylinder).

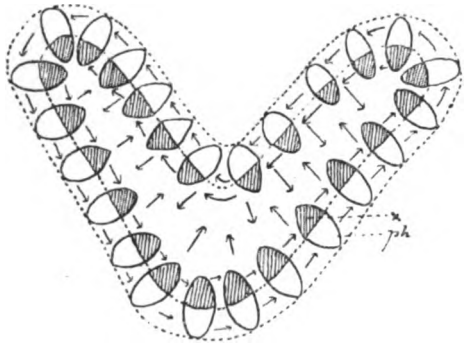

FIG. 15. Diagrammatic representation of method of derivation of the numerous, separate, collateral bundles of petiole of Cycads from the single, large, concentric bundle of petiole of *Lyginodendron*, &c. (transverse section).

The bundles in the petiole of, e. g. *Encephalartos*, are precisely identical, both as regards orientation, number, and *individual structure*, with those of *Myeloxylon*. The similarity, indeed, is so close as to render an homology between the two systems of bundles practically certain. If this be admitted, it must then of necessity follow (a conclusion which appears hitherto to have been completely overlooked) that the *vascular systems* of the *stems* of *Medullosa* and Cycads respectively must also be homologous. And if this be so, what becomes of the theory which regards the Cycadean central cylinder as having been derived from the single *Heterangium* stele?

At first sight it would seem as if no relation whatever existed between the vascular structure of the leaf-petiole of *Lyginodendron* or *Heterangium* and that of the same organ in *Medullosa* and the Cycads. The single [2]

[1] In the case of the male sporophyll a *single* bundle leaves the cone-cylinder which subsequently in the cortex branches into two.

[2] In some cases there are two bundles.

large bundle of *Lyginodendron*, with its *several* protoxylem-groups situated in a mesarch position, really, in my opinion, corresponds to, and is the equivalent of, a *number* of collateral mesarch bundles united together by means of their *centripetal* xylems, their phloems likewise fusing and surrounding the whole. If we imagine each of these primary centres separated, each constituting a distinct bundle and at the same time retaining its position, they would be seen to roughly exhibit the horse-shoe-shaped grouping so characteristic of most Cycads (Fig. 15). This grouping most closely resembles that of the bundles in the petiole of *Stangeria*; and this is interesting, for the foliage of *Stangeria* is the most Fern-like of all Cycadian leaves (Fig. 16). The extreme case of subdivision of such a *Rachiopteris*-strand is seen in the petioles of *Medullosa* (*Mycloxylon*) and certain species of *Encephalartos* (e. g. *E. cycadifolius*) where an enormous number of separate collateral bundles exist, orientated in a variety of directions. But in *E. horridus* we note a case which, in my opinion, represents a distinct transition to the monodesmic condition of *Lyginodendron*; for here the vascular system represents a modification of the Ω in which the bundles are *fusing together in groups* in a *radial* direction, i. e. *towards the centre* of the organ, to form small, usually imperfectly, concentric strands. We have only to imagine this phenomenon proceeding still further in order to obtain a petiolar vascular system consisting of one or two large concentric bundles as in *Lyginodendron*. In the case of *Stangeria* we see *lateral* fusion between the bundles taking place, which, of course, would also be necessary in order to build up the primitive large concentric strand; so that I am inclined to regard all these examples of fusion as *reversions* to an ancestral condition (Fig. 16).

FIG. 16. *Stangeria paradoxa*: diagrammatic transverse section of vascular system of petiole, showing lateral fusion of bundles (after Matte).

If the view here set forth be adopted the two sets of petiolar vascular systems represented by Cycads on the one hand and *Lyginodendron* and *Heterangium* on the other, become easily related and harmonized. Ever since I first observed them, some nine years ago now, I have always regarded the *mesarch* collateral bundles of the Cycadean petiole as a remnant of a former concentric strand possessing a central mass of centripetal xylem in the common, far-back ancestors of the Cycads and the Medulloseae. I regard the single polyarch bundle of *Lygino-*

dendron, &c., as the most *primitive* of the two types of petiolar bundle-systems for the simple reason that it is the most *Fern-like*; one has only to recall the single, concentrically-constructed petiolar bundles of such Ferns as *Zygopteris*, *Osmunda*, *Ophioglossum*, &c., to render this view reasonable.

The fact that the leaf-trace of *Medullosa*, on its first leaving the vascular system of the stem, is a single concentric bundle which subsequently becomes fragmented into a number of collateral bundles, each having precisely the structure of the petiolar bundles of modern Cycads, is further evidence as to the original ancestral character of the petiolar vascular system of these modern plants; this is another good example of the first-formed tissues in the ontogeny exhibiting ancestral characters, for we must regard the lowest part of the leaf-trace as, ontogenetically, the most primitive.

The Sphenopteroid foliage of *Lyginodendron* and *Heterangium* may also be said to be *less Cycad-like* than the Alethopteroid and Neuropteroid foliage of the Medulloseae.

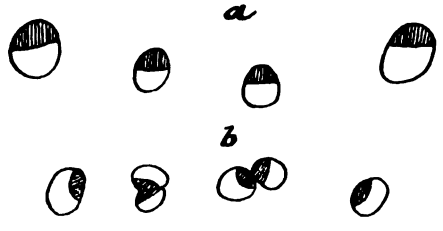

FIG. 17. *Zamia Lindeni*: diagrammatic transverse section of vascular systems of fertile (*a*) and sterile (*b*) sporophylls respectively, showing difference in orientation and structure of the strands in the two systems.

Another point is worth remarking: there is always a tendency for the separate collateral bundles, which I regard as the individual units resulting from the above-described fragmentation, to become each one concentric in structure, as if partaking of the character of the parent-bundle in the stem from which they sprang. This is the probable cause of the arc-shaped phloem of all foliar bundles in Cycads. Hence the concentric bundles of the cotyledons of *Stangeria* and *Bowenia*, of many sporophylls and, in some cases, of the integuments.

It is not unlikely that in the vascular systems of the petioles of the Cycadophyta [1] all stages and types occur between the single large concentric bundle of *Lyginodendron*, &c., and the numerous collateral bundles of *Myeloxylon*, just as in the vascular system of the stems of the Medulloseae and Cycads the types range from the single solenostele of *M. porosa*, through the ring of numerous concentric bundles or steles, to that of the numerous collateral strands of a modern Cycad.

In the case of the sporophylls the primitive concentric structure tends wholly to disappear, as a rule, in those bundles which are functional

[1] I am here using this term, for the first time, in a new sense, viz. to include the Pteridosperms, the Mesozoic Cycadales, and modern Cycads; whereas Nathorst's use of the term included only the two latter groups; the Cordaites are, for the time being, at any rate, left out of consideration.

in supplying the sporangia. The others, however, generally show some sign of it. It is highly interesting to find that the *sterile* sporophylls at the base of the cone contain bundles which, no longer compelled to submit to the above-named adaptive modification, revert back and tend to assume the concentric structure of the past (Fig. 17).

The girdle-like character of the leaf-trace system in the stems of modern Cycads is a recently-adopted modification; for in the Medulloseae and *Lyginodendron*, as also in the Bennettiteae, the leaf-traces pursue a directly radial course to the cylinder; I noticed with much interest that this was also the case with the traces passing in from the *cotyledons* in a seedling of *Cycas*; and the same thing is seen in the case of the sporophyll-traces of the cones. These four sets of facts prove that the radial course of the leaf-traces is the *ancestral* condition of affairs.

As regards the morphology of the foliar organs and the mode of insertion of the sporangia: both foliage-leaves and sporophylls, in view of the Pteridospermic ancestry of the Cycads, must be regarded as organs which have become reduced in complexity of outline from the condition of the Fern-like foliar organs of the past. The decompound foliage-leaves of the Pteridosperms have become transformed into mere pinnately-divided organs in the modern forms[1]. In the former (e.g. in *Lyginodendron* and Neuropterideae) it would appear that both male and female sporangia were borne as *terminal* organs on ultimate subdivisions of a decompound[2], *dorsiventral* foliar organ which was either assimilating or not.

This terminal position of the reproductive organs I regard as an ancient primitive character, a reminiscence of the remote period when not only these ultimate ramifications of the sporophyll, but the entire organ itself, possessed *radial symmetry*[3]; for I follow Čelakovský's view that all foliar organs, including even such highly complex dorsiventral forms as the Fern-leaves, have sprung originally from the sympodially-grouped reproductions or repetitions of a bryophytic sporogonium. Traces of this primitive character may still be found in some of the recent Ferns, such as Hymenophyllaceae, Schizaeaceae, Cyatheaceae.

In the group Bennettiteae the radial symmetry in the female sex is possessed by the entire sporophyll bearing the seed in a terminal position. Whether this 'cone,' considered in its entirety, is a reduced or a primitive structure we have, at present, no means of determining. On the male side the sporophyll appears to possess a dorsiventral structure with superficially-placed sporangia. In *Cycadospadix* the sporangia on the female side also seem to occupy a superficial position.

[1] *Cycas Micholitzii*, Dyer, recently imported from Annam, differs from all other known species of that genus in possessing repeatedly-dichotomizing pinnae, and hence probably represents a more ancient type of leaf than the ordinary simply pinnate form.

[2] Possibly some were of much simpler conformation.

[3] Cf. male and female sporophylls of Cordaiteae.

Having regard to the Neuropteridean affinities of modern Cycads I should consider their *cones* as the final result of an extreme reduction of the erstwhile complex sporophylls, combined with a compact aggregation of these latter on a special portion of the main axis of the plant[1]. The sporophylls still retain a dorsiventral symmetry. On the female side the sporangia may be said to have just lost their primitive terminal position, for they are no longer on the actual margin but on the lower *surface* of the sporophyll. On the male side they are situated entirely on the lower surface, with no suggestion of a former marginal position, except in the case of *Zamia*, where they occupy much the same position as do the ovules on the female side. The genus *Cycas* is of great interest, for whereas the male sporophylls are reduced and arrayed in a cone, as in other genera, the female sporophylls constitute appendages of the vegetative portion of the stem. They are distinctly leaf-like, bear rudimentary pinnae in their upper portion, and a larger number of ovules than in the case of other genera. These ovules are also more primitive both as regards their size and also as to their position on the sporophyll, for they are borne *terminally* on extremely short, lateral outgrowths of the rachis, which may be regarded as the equivalents of the pinnae in the upper portion of the organ. Hence we may consider the female sporophyll of *Cycas* as approaching much more closely that of its Pteridospermic ancestor than is the case with other Cycads.

I formerly regarded the question as to the origin of the Cycadean sporophylls from a much too general standpoint. From the point of view of plant-evolution as a whole, I believe my statements will still hold good, but will require some modification as regards the minor cycle of evolution which concerns the Cycads alone. In 1898 I stated that 'the original type, viz. that in which the sporangiferous organs were distinct from the assimilating leaves, probably persisted right through, even down to the present day. From such forms as these latter I imagine it to be quite conceivable, and even probable, that modern Cycads took their origin.' In the light of recent discoveries as to the origin of Cycads this statement must now be retracted.

In conclusion, I may say one word as to the morphology of the ovular envelopes. I must side wholly with Čelakovský in maintaining that the law of uniformity demands that throughout Gymnosperms, to say nothing of higher and lower plant-forms, the sporangium must possess *two* integuments or the equivalents of such. In the ovule of Cycads there is no obvious representation of these; yet the comparison of the seeds of *allied* forms, both fossil and recent, show that two integuments are probably present, although so intimately and congenitally concrescent as to give to the whole envelope the appearance of a primæval integrity. In *Lagenostoma*, the

[1] This may have also happened in the case of *Bennettites* on the *lateral* branches.

seed of *Lyginodendron*, as also in that of *Neuropteris heterophylla*, the outer integument is probably represented by the detached cupule, while the inner integument itself is a hard sclerotic envelope. In *Trigonocarpus* there was an outer fleshy layer concrescent with an inner bony envelope, just as in modern Cycads. The same was also probably the case with *Stephanospermum*.

In *Taxus* the fleshy layer is detached in the form of an aril. Hence I am led to regard the outer fleshy layer in the ovule of Cycads as representing the *outer* integument, and the sclerotic layer and inner soft-celled tissue as together constituting the *inner* integument.

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On the Seedling-Structure of certain Piperales.

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With Plate X and three Diagrams in the Text.

THE completion of the investigation, started some time ago[1], on the structure of the seedlings of certain Piperales, has been much handicapped by the difficulty experienced in obtaining seeds; and the failure, in many cases, of these, when procured, to germinate. However, sufficient material has now been examined to warrant publication.

The cohort Piperales is of interest, inasmuch as it is characterized by certain features shared in common with many Monocotyledons. Thus Campbell[2], comparing certain Araceae with *Peperomia*, remarks, 'in the form of the leaves and inflorescence, as well as in certain anatomical characters, e.g. the distribution of the vascular bundles in the stem of *Peperomia*, there are very curious parallelisms. The structure of the flower and position of the ovule are also similar.'

In a later paper[3] he further expresses his opinion that 'the resemblances in general habit, as well as the distribution of the vascular bundles in *Peperomia* and the Araceae, might indicate a remote relationship between them; the presence in the latter of nucellar tissue, which might be compared to the perisperm of the Piperaceae, might be cited as further evidence of a possible relationship.... The possibility of a connexion with some of the lower Dicotyledons through forms like *Peperomia* may fairly be considered worthy of consideration.'

And further, in writing of *Peperomia*[4], our author makes the following statement: 'From a study of many low types among the Monocotyledons, which cannot be readily derived from higher types, e.g. *Naias*, many Araceae, it seems more reasonable to consider the single carpel with

[1] Hill, T. G. New Phytologist, Vol. iii, February, 1904.
[2] Campbell, D. H. Studies on the Araceae, I. Ann. Bot., xiv, 1900, p. 22.
[3] „ „ Studies on the Araceae, III. Ann. Bot., xix, 1905.
[4] „ „ The Embryo-sac of Peperomia. Ann. Bot., xv, 1901.

a single axial ovule as the primitive type for the Angiosperms, and with this *Peperomia* agrees perfectly.'

Thus it is obvious that in the light of recent research, more especially as regards questions dealing with the Phylogeny of the Angiosperms, the plants herein dealt with are of some importance.

PIPERACEAE.

Piper cornifolium, H. B. K. The basal region of each seed-leaf possesses one comparatively large collateral vascular bundle (Fig. 1) which enters the petiole, when almost immediately a redistribution of the constituent tissues gradually takes place. The phloem is resolved into two masses, bounding the xylem on either side, and, at the same time,

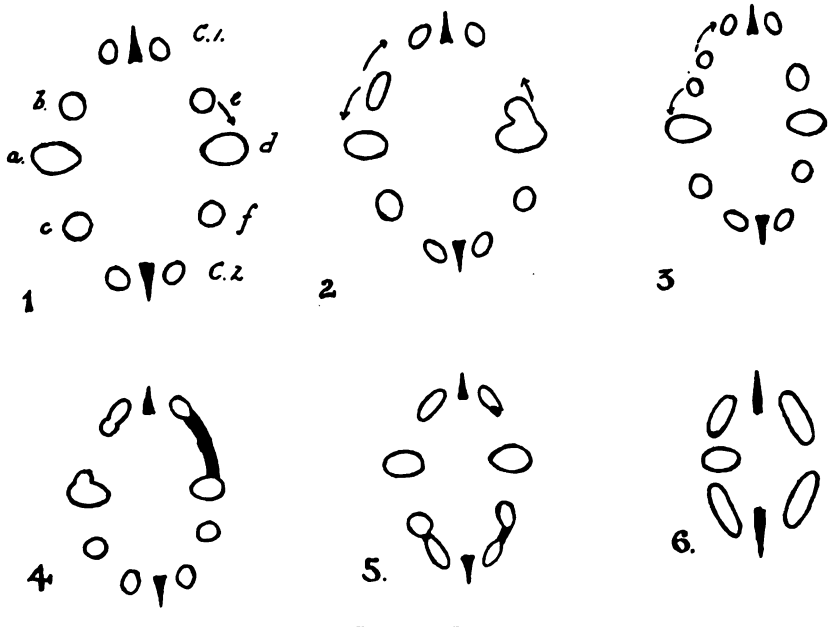


DIAGRAM I.

Illustrating the anastomoses which occur between the phloem of the cotyledon bundles *C.* 1, *C.* 2, and the epicotyledonary strands *a*, *b*, *c*, *d*, *e*, and *f*. In the cotyledon-traces the exarch protoxylem is bounded on each side by a group of phloem elements.

the xylem undergoes rotation, so that the protoxylem becomes exarch, whilst the bundle is still within the petiole of the cotyledon (Figs. 2 and 3). At the cotyledonary node the bundles enter the axis and pass towards the centre, which, in the oldest seedling examined, possessed six bundles derived from the plumule. These epicotyledonary traces exercise no influence on the transition phenomena, and were, for the most part, still merismatic, one only containing lignified elements. They are arranged in

two groups, each consisting of three strands, the largest bundles occupying a central position in their respective group. Anastomoses take place between these plumular traces and the two phloem masses of each cotyledon-bundle, the exact junctions being illustrated in the accompanying Diagram I, from which it will be seen that, essentially, the lateral bundles, *b*, *c*, *e*, and *f*, fuse with the nearest cotyledonary phloem mass, and then the four phloem groups thus formed take up a more central position, the neighbouring phloems joining up to form two groups. The protoxylem is already exarch, and occupies its proper position relative to the bast; thus a typical diarch root obtains (Figs. 4, 5, and 6, Plate X).

It has already been pointed out by Tansley and Thomas [1] that this is an extreme case of what obtains in other plants. They themselves 'have found this type in fourteen genera of Ranunculaceae, in certain Berberidaceae, and in every genus examined (twenty-four in all) belonging to the orders Papaveraceae (including Fumariaceae), Capparidaceae, Resedaceae, and Cruciferae'. Sterckx [2], Gérard [3], Miss Sargant [4], and Tansley [5] have described the same type as occurring in certain Ranunculaceae and allied plants; Miss Sargant [4] and Chauveaud [6] have drawn attention to the presence of a similar type in a number of monocotyledonous plants, and, finally, the writer has found it to obtain in certain Centrospermae. Further research will show whether the type is of more general occurrence throughout the Dicotyledons.

One of the seedlings examined possessed three cotyledons, the plumule was in an embryonic state, and its vascular bundles were much less developed than in the plant just described.

The transition in this tricotyledonary specimen followed precisely similar lines to those described for the normal plant. At the cotyledonary node each bundle with its bifurcated phloem and exarch protoxylem passes inwards, and, as they do so, the phloem groups of each bundle separate more and more, until each ultimately comes into contact with a phloem group of one of the other cotyledonary traces, so that finally three phloems result. The xylem strands converge towards the centre of the

[1] Tansley, A. G. and Thomas, E. N. Root Structure in the Central Cylinder of the Hypocotyl. New Phytologist, Vol. iii, No. 4, April, 1904.

[2] Sterckx. Recherches anatomiques sur l'embryon et les plantules dans la famille des Renonculacées. Mem. Soc. Roy. Sci. Liège, sér. 3, t. ii, 1899.

[3] Gérard, R. Recherches sur le passage de la Racine à la Tige. Ann. Sci. Nat. Bot. sér. 6, t. xi, 1880.

[4] Sargant, E. A Theory of the Origin of Monocotyledons founded on the Structure of their Seedlings. Ann. Bot., xvii, 1903.

[5] Tansley, A. G. Reduction in Descent. New Phytologist, Vol. i, 1902.

[6] Chauveaud, M. G. Passage de la position alterne à la position superposée de l'appareil conducteur, avec destruction des vaisseaux centripètes primitifs, dans le cotylédon de l'Oignon (Allium Cepa). Bull. du Mus. d'Hist. Nat., No. 1, 1902, p. 52.

Chauveaud, M. G. Sur le passage de la disposition alterne des éléments libériens et ligneux à leur disposition superposée dans le Trocart (Triglochin). Bull. du Mus. d'Hist. Nat., No. 3, 1901, p. 124.

axis in a straight line, and obviously occupy positions between the phloem masses: thus a triarch root is produced. These changes do not end here: normally, of course, two seed-leaves are present, and the root is diarch; in this case there are three cotyledons, and the root is triarch.

On the examination of the root at a lower level it is seen that the triarch structure becomes diarch. The changes leading to the alteration are illustrated in Diagram II.

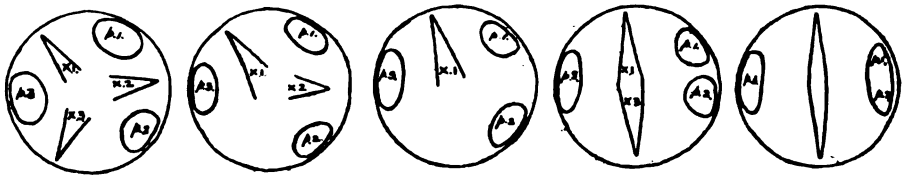


DIAGRAM II.

Terming the xylem and phloem groups *X.* 1, *X.* 2, *X.* 3, *p.* 1, *p.* 2, and *p.* 3, respectively; one xylem mass, *X.* 3, temporarily disappears, and this is followed by the obliteration of the group *X.* 2. So that, at this stage, there obtains, as regards the xylem, a monarch structure. The phloems *p.* 1, *p.* 2 now approach one another to form a single strand, and, at the same time, the xylem ray, which was the first to disappear, reappears. Thus there results a diarch root.

Piper geniculatum, Hort. ex Link., follows a precisely similar course, even to the behaviour of the epicotyledonary traces.

Peperomia eburnea, Linden. At the distal end of the petiole of each cotyledon the bundles of the blade fuse together to form a single strand, the behaviour of which is not necessarily the same in each petiole. In one seedling it was found that in one petiole there was a normal collateral bundle with endarch protoxylem; tracing this strand downwards, no bifurcation of the phloem occurs, but the strand, as a whole, becomes somewhat obliquely orientated with the greater mass of phloem on one side, and also with the smallest xylem element somewhat more exarch than its neighbours. Immediately above the cotyledonary node this bundle shows its xylem tangentially arranged, and its phloem in an early stage of bifurcation.

Turning now to the other cotyledon, the bundle is found, at the distal end of the petiole, to be somewhat *U*-shaped, the xylem forming a tangential row of elements between the two groups of phloem elements. At a lower level, the xylem of this strand undergoes rotation, so that by the time the node is reached the bundle has its protoxylem exarch and its phloem in two masses. These differences will be realized by the examination of Figs. 7, 8, and 9, of which the two first illustrate the appearance of the two bundles at the same level. As the cotyledonary traces pass inwards towards the centre of the axis, the phloem of the bundle first described separates into two well-defined masses, corresponding to what obtains in the other. The course now followed is the same as in *Piper*, except that as regards the bundle first described no rotation of the xylem

could be made out; if it takes place, it must do so during its inward passage from the node, but what probably occurs is that the metaxylem elements overtake and pass the protoxylem, so that the latter become exarch. A diarch root-structure is thus formed directly the two strands meet in the centre of the axis.

Other seedlings showed what is probably the normal course, viz. each endarch bundle of the cotyledon petiole, as it passes downwards towards the node, exhibits a bifurcation of the phloem and a rotation of the xylem as described for *Piper*, but this rearrangement in *Peperomia eburnea* is not nearly so decided as in *Piper*.

A further anomaly was exhibited by another seedling of this same species; the cotyledonary bundles showed the normal rearrangement, but one also possessed a group of phloem elements on the protoxylem side of the strand. This extra phloem decreased in amount, so that by the time the centre of the axis was reached it consisted of but a few elements which still retained their abnormal position internal to the protoxylem. Ultimately they entirely disappeared.

This same specimen was also peculiar, inasmuch as a normal root-structure took much longer to form than in other individuals of the same species.

Peperomia pellucida, H. B. K. One vascular bundle enters the distal end of each petiole from the cotyledon (Fig. 13). Tracing the strand downwards, the phloem gradually forms two groups of elements as in *Pep. eburnea*, but frequently this bifurcation is not equally well marked in the bundle of each seed-leaf petiole. Immediately before the node is reached there is a suggestion of the protoxylem taking up an exarch position.

The cotyledonary traces pass inwards as relatively broad bands; the phloem groups of each strand separate and pass to opposite sides of the central cylinder, where they come into contact with the plumular bundles which, in the youngest seedling examined, were still in a procambial state and arranged in two groups, one on each side of the central cylinder, and separated by parenchymatous elements. Thus the two phloems of the root result.

Concurrently, the xylem follows a centripetal course, the metaxylem travels further inwards, thus leaving the protoxylem in an exarch position; these elements are very few in number, there being one on one side and two on the other. The tracheae are irregularly disposed, and there is no diarch plate such as obtains in *Piper*, at about this stage (Fig. 14).

Following these structures downwards, new xylem elements may make their appearance external to, and in contact with, the existing protoxylem. Further, it is seen that these elements follow an undulating course, so that in one transverse section they may be in contact with the metaxylem

tracheae, and at a lower level they may be separated from them by two or three parenchyma cells. Finally, however, the two protoxylem groups come into contact with the metaxylem elements, which range themselves in line, so that a typical diarch plate obtains.

In older seedlings the epicotyledonary axis has six bundles, three derived from each of the two foliage leaves, arranged roughly in a circle. Much anastomosing and redistribution take place between these traces, as a result of which there are formed two strands, separated one from the other by parenchyma, and situated at right angles to the line joining the two cotyledonary bundles. As soon as this arrangement is effected the seed-leaf traces enter the central cylinder in the manner already described.

In these older seedlings more metaxylem is derived from the plumule than from the cotyledons, but these elements rapidly disappear, so that at the slightly lower level the lignified elements obtaining are those derived from the seed-leaves.

Peperomia polystachya, Hook. The material of this plant was not entirely satisfactory, inasmuch as very few of the seedlings retained their cotyledons. Thus it was not possible to follow the course of the bundle from the cotyledon to the petiole. Sufficient, however, was made out to indicate that, as regards the behaviour of the bundles of the seed-leaves, this species occupies a position intermediate between *Pep. pellucida* and *Pep. amplexifolia*. At the base of the petiole of each seed-leaf a single strand may be seen with its protoxylem in an endarch position, and its phloem spread out tangentially and somewhat bilobed.

Immediately before its entry into the axis the metaxylem may be seen to be separated into two masses by parenchyma, but no rotation of the protoxylem can be made out.

When the plumule is well developed the bundles of the third internode are markedly arranged in two whorls, six strands in the outer, and four in the inner. At the node below the incoming traces fuse with certain of these bundles, and anastomoses occur between the vascular strands of the two whorls, so that in the second internode there obtain three bundles in the inner and six in the outer ring. Similar junctions take place at the node below, resulting in the formation of a single strand centrally placed and surrounded by a zone of five. These bundles join up with one another, hence there result four epicotyledonary strands, two on one side and a similar pair on the opposite side of an imaginary line joining the two incoming cotyledonary traces.

As the seed-leaf bundles approach the centre of the axis the phloem of each separates into two masses which fuse with the phloem of the nearest plumular trace. This branching of the cotyledonary bast is sometimes very unequal, for nearly all the phloem from one bundle may go to one of the pair of plumular bundles.

The xylem, small in amount, of the seed-leaves pursues a straight course, and comes into contact with the protoxylem of the plumular strands, the two then being practically indistinguishable.

The four epicotyledonary bundles fuse in pairs, to form two large pyriform strands. Lower down, the central cylinder loses its oval shape and becomes rounded in outline. At the same time the metaxylem becomes less abundant, and, at a still lower level, the central xylem gradually takes up a position nearer the endodermis; the smallest elements, however, do not occupy an exarch position. Thus a really typical root-structure does not obtain; the plant under consideration resembling, in this respect, *Pep. maculosa* and *Pep. tithymaloides.*

Peperomia amplexifolia, A. Dietr. The petiole of each seed-leaf has the usual single bundle. These strands are small as viewed in transverse sections, each being no larger than one of the surrounding parenchyma cells. No bifurcation of the phloem nor rotation of the xylem takes place, as in the plants hitherto described. The cotyledonary traces enter the axis as normal collateral structures. In one plant it was noticed that at the base of the seed-leaf petiole the strands were placed obliquely to the dorsoventral line of the cotyledon; but this did not obtain in the other individuals examined.

Another feature of interest is the fact that the free edges of the bases of the petioles of the seed-leaves fuse, so that there is formed a cotyledonary tube around the axis.

The oldest seedling examined possessed two young foliage leaves, each having three bundles, one large and central, with lignified elements, and two smaller, lateral in position, and more or less merismatic.

The traces of the youngest leaf enter the axis and fuse with the merismatic central cylinder. At a slightly lower level the bundles of the leaf are seen alternating with three small merismatic strands, which are situated nearer the centre. At the node next below the bundles of the oldest leaf enter, so that there result two well-marked zones of bundles. Those of the oldest leaf move centripetally, so that at the cotyledonary node the strands no longer exhibit a scattered disposition. Fusions now take place between the various plumular traces, as a result of which four vascular strands are formed. During these changes the cotyledonary bundles have entered the axis, and occupy a position one on each side of the group of plumular traces. One cotyledon-trace fuses with the nearest epicotyl-bundle; the metaxylem and phloem of both coming into contact, and the protoxylem of the seed-leaf being somewhat isolated. Further junctions take place between the plumular traces, so that two large bundles result. The other cotyledon-trace now fuses up, its phloem dividing into two unequal strands, the largest of which joins with the bast of the bundle alternate to that with which the first cotyledon-trace fused,

and the protoxylem occupying a position corresponding with that taken up by the same tissue of the opposite seed-leaf. As soon as these changes (the details of which are figured in Diagram III) have been effected, an endodermis puts in an appearance, and the central strand has a typical root-like appearance.

The fact that the two cotyledon-bundles fused with the plumular

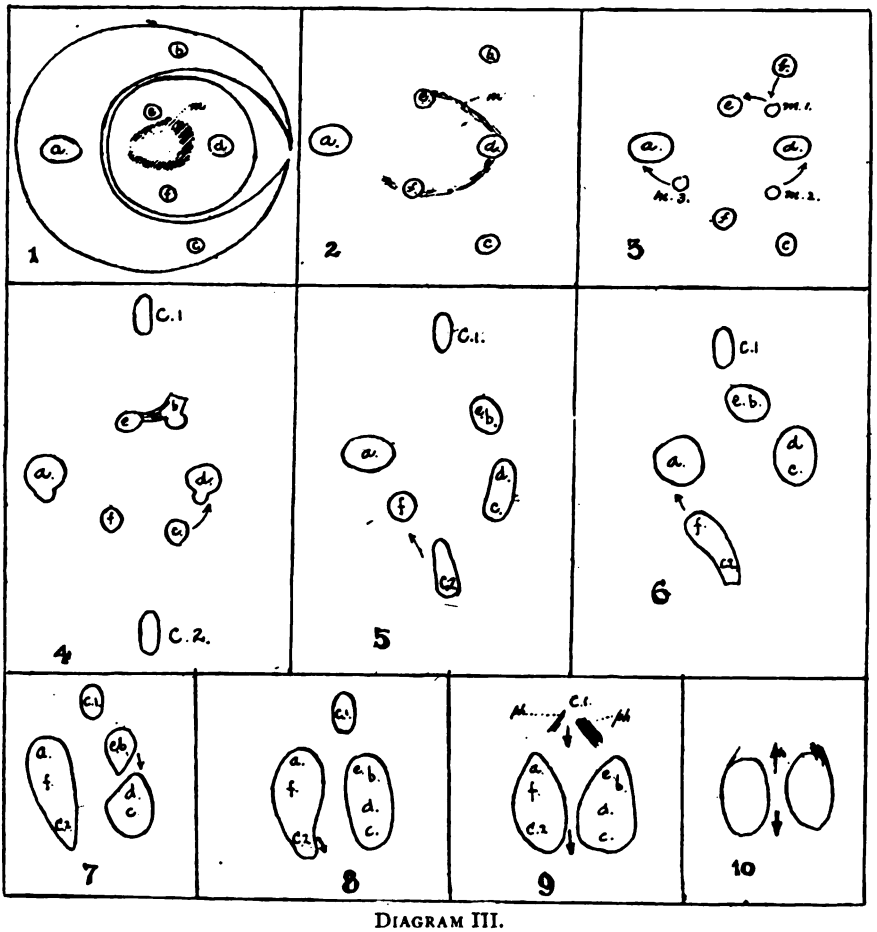


DIAGRAM III.

a, *b*, *c*, *d*, *e*, *f*, plumular bundles; *m*, merismatic tissue; *m.* 1., *m.* 2., *m.*, 3., merismatic bundles; *C.* 1., *C.* 2., cotyledon-traces; *ph.*, phloem. The heavy arrows indicate the protoxylem of the cotyledon-traces.

traces at slightly different levels is probably to be accounted for by the cotyledons themselves being inserted at slightly different levels.

There is no definite rotation of the protoxylem elements; they seemingly occupy their exarch position owing to the fact that the metaxylem moves away from and leaves them isolated, a reunion being afterwards effected.

On comparing these changes with those obtaining in *Arum maculatum*[1], many points of similarity are to be found, more especially as regards the zoning and fusions of the plumular traces, and the method of union of the cotyledon-bundles with these strands. But, at the same time, it must be pointed out that a certain amount of variation obtains in *Pep. amplexifolia*: thus, in a seedling of about the same age as the one just described, it was found that, although the youngest foliage leaf contributed the normal number three, only one bundle entered the axis from the oldest foliage leaf, so that instead of having two zones of bundles the axis had an irregular ring of four strands.

At a level slightly below the cotyledonary node intercommunications take place between the plumular traces, resulting in the formation of two bundles somewhat obliquely situated, and with their xylems separated by a thin layer of parenchyma. This arrangement is effected immediately before the entry and fusion of the cotyledonary traces, which enter the axis and travel to the central vascular strand as collateral structures. Immediately before fusion the phloem of each branches to the right and left of the xylem, and comes into contact with the bast of the epicotyl-bundles, while the xylem behaves in the manner already described.

Both in this and in other species it is sometimes found that the phloem of the cotyledonary traces divides into two very unequal strands, so that one side of the vascular cylinder may sometimes receive nearly the whole of the phloem of one seed-leaf bundle.

Peperomia tithymaloides, A. Dietr. All the seedlings examined had a well-formed plumule with three foliage leaves. The structure of the epicotyl is similar to that of *Pep. amplexifolia*, as regards the definite zoning of the bundles, and the anastomosing of these structures at the nodes. The chief difference lies in the fact that the number of the leaf traces is rather more variable in *Pep. tithymaloides*. Thus, in one plant, the youngest leaf had four traces, the next youngest three, and the oldest only one; three strands, however, appear to be the typical number.

The cotyledonary bundles are small, single, and collateral (Fig. 10); and, as in *Pep. amplexifolia*, and the species described hereafter, there is no bifurcation of the phloem, nor rotation of the xylem. Immediately before the entry of the seed-leaf traces the plumular strands are arranged in an elliptical zone, three being on one side and three on the opposite side, the largest of each group being bounded by the smaller. The cotyledonary bundles enter and occupy positions corresponding to the foci of the ellipse. The phloem of these branches to the right and left of the xylem, and, passing inwards, fuses with the corresponding tissue of the plumular strands, while the metaxylem travels towards the centre and effects a junction with

[1] Scott, R. and Sargant, E. On the Development of Arum maculatum from the Seed. Ann. Bot., xii, 1898.

the xylem of the plumular bundles, thus forming a somewhat irregular plate. Concurrently, the three epicotyledonary bundles of each side fuse, so that there result two large collateral structures, one on each side. The two protoxylem groups derived from the cotyledons retain their relative and isolated position for some time, having a crushed appearance, some being almost entirely obliterated (Fig. 11). Ultimately, these protoxylem groups come into contact with the xylem of the plumular strands; at a still lower level an endodermis is differentiated, and the vascular tissue decreases in amount (Fig. 12).

Peperomia maculosa, Hook. The transition phenomena are essentially the same as in the last species dealt with. The differences which obtain are unimportant, and are briefly as follows. At the level of the insertion of the seed-leaves the epicotyledonary strands are five in number, three in one group and two forming the corresponding opposite group; whereas in *Pep. tithymaloides* there are six bundles arranged in threes. Further, the phloem of the seed-leaf traces branches somewhat earlier in *Pep maculosa*. And again, in the last-named plant, all the xylem, with the exception of one element of the cotyledonary strands, passes to the centre of the vascular cylinder, fusing one with the other and with the wood of the plumular bundles, which, by this time, have formed two large pear-shaped structures. The elements left behind occupy a solitary position well towards the periphery of the stele, one on each side, and they independently follow an undulating course downwards; so that a diarch plate, small and not well defined, may result at one level, while at a lower level the plate may exist on one side and not on the other.

One seedling exhibited a curious anomaly, which resulted in a seemingly unnecessary redistribution of vascular tissue.

Towards the base of the axis a strand of phloem was given off from one of the phloem masses of the central cylinder. The strand followed a downward spiral course, passing on the outside of the protoxylem, and receiving elements from the metaxylem in its passage, thus appearing as a collateral structure, but quickly becoming somewhat more root-like by a rearrangement of the phloem; but instead of emerging as a lateral root it pursued its spiral course, circling around to the side from whence it came, and ultimately fused with the vascular cylinder.

It may be added that a lateral root does, in this species and in others, sometimes arise directly opposite a phloem group.

From the foregoing account it is clear that the species of *Peperomia* examined fall into two divisions. In the first may be placed *Pep. eburnea* and *Pep. pellucida*, both characterized by the occurrence of a certain amount of rearrangement in the cotyledonary bundles, while still contained within the petiole; and in the second, *Pep. polystachya*, *Pep.*

amplexifolia, *Pep. tithymaloides*, and *Pep. maculosa*, in which no such rearrangement takes place. These two groups merge imperceptibly one into the other; and further, a gradual reduction in the transition phenomena may be traced from *Piper cornifolium*, which forms one extreme, to *Peperomia tithymaloides*, which forms the other extreme. In the first case the vascular tissue of the root is derived chiefly from the cotyledons, while in the last the seed-leaf traces are unimportant; the plumular bundles playing the prominent part.

The absence of rotation in the xylem of the seed-leaf bundles is seemingly not confined to *Peperomia*. Chauveaud [1] has described what appears to be a similar case in the Labiatae. He remarks: 'Dans le *Lamium album* . . . les deux faisceaux ligneux primaires de la radicule se continuent jusque dans les cotylédons, en demeurant toujours dans le même plan, qui est le plan de symétrie des cotylédons. Ces faisceaux ne se partagent pas en deux masses et aucune rotation n'intervient.'

SAURURACEAE.

Houttuynia cordata, Thunb. The transition phenomena are similar to those already described for *Peperomia*. The petioles of the seed-leaves form a short tube round the axis; each contains one bundle, which, throughout its course, remains collateral with its protoxylem endarch in position. These bundles have their xylem but feebly developed, there being not more than two or three elements in each strand. On arriving near the centre of the axis the phloem branches to the right and left of the xylem, the corresponding groups fusing to form the two phloem masses of the roots. Concurrently, during the inward passage there is seemingly a rearrangement of the xylem, which results in the smallest elements being exarch in position. Metaxylem appears; a root-structure with a typical diarch plate results (Figs. 16 and 17).

In older seedlings the cotyledonary tube is better marked, and their bundles have more xylem (Fig. 15).

The plumular traces fuse together, forming two fairly large collateral bundles occupying the centre of the axis, one on each side. As in *Pep. polystachya* and *Pep. amplexifolia*, the bifurcation of the cotyledonary phloem is very unequal, sometimes almost non-existent, inasmuch as practically the whole of this tissue from one seed-leaf bundle may fuse with the bast of one of the two plumular strands. This inequality of distribution is most marked in the older seedlings, and the reason for its occurrence may be to render each phloem group of the root equal in size.

The xylem of the cotyledon-bundles of the older seedlings behaves in the manner already described: there is, however, a certain amount of

[1] Chauveaud, M. G. Sur la persistance de la structure alterne dans les cotylédons du Lamier blanc et de plusieurs autres Labiées. Comptes Rendus, 21 mars 1904.

variation. The protoxylem may become exarch during the inward passage; sometimes the final disposition is reached by the dying out of the accompanying metaxylem. Further, in one case, it was observed that the cotyledonary xylem enters the central cylinder as an endarch mass, the exarch position of the protoxylem being arrived at by the metaxylem bending round and taking up a morecentral position.

The transition takes place very quickly, and an endodermis makes its appearance directly it is accomplished.

Saururus cernuus, Linn. The petioles of the cotyledons form a tube round the axis as in *H. cordata*, and, as the transition phenomena are also identical with those of the latter, no detailed description is called for.

The only point to be remarked is that in one plant the phloem of the bundle of one cotyledon, not of the other, exhibited a bifurcation in the base of the petiole.

Houttuynia and *Saururus* thus resemble *Peperomia*, and they, together with *Piper*, on the whole, conform to Van Tieghem's type 3.

Theoretical.

The first question of theoretical interest is whether *Peperomia* is to be considered as a primitive or a reduced form. Campbell[1] maintains that in *Peperomia* we have to deal with the most primitive type of Angiosperm yet discovered, and that the peculiarities of the embryo-sac are not reductions, but consist of an increase in the number of parts. On the other hand, Johnson[2] in his work on the embryo-sac of *Peperomia* expresses himself as follows: 'That these peculiarities are to be considered primitive rather than higher specializations seems to me unwarranted by the evidence at present available, especially when we consider the fact, which I have ascertained, that such closely related genera as *Piper*, *Heckeria*, and *Saururus*[3] have essentially typical angiosperm embryo-sacs. . . . I am inclined to believe that the peculiarities of the embryo-sac of *Peperomia* have been secondarily acquired, and are analogous to those found in other angiosperms of peculiar habit, e.g. many aquatic, parasitic, and saprophytic forms.'

Finally, Johnson[4] has recently expressed the opinion that the development of the megasporangium and the female gametophyte of Angiosperms is an unsatisfactory index of genetic relationship, inasmuch as it may vary

[1] Campbell, D. H. Die Entwickelung des Embryosackes von Peperomia pellucida. Ber. d. deut. Bot. Gesells. xvii, 1899.

Campbell, D. H. The Embryo-sac of Peperomia. Ann. Bot., xv, 1901.

[2] Johnson, Duncan S. On the Endosperm and Embryo of Peperomia pellucida. Bot. Gaz., xxx, 1900.

[3] Johnson, Duncan S. On the Development of Saururus cernuus. Torrey Bot. Club Bull., 1900. See also On the Development of certain Piperaceae. Bot. Gaz., xxxiv, 1902.

[4] Johnson, Duncan S. Seed Development in the Piperales and its bearing on the Relationship of the Order. Johns Hopkins Univ. Circ. No. 178, 1905.

considerably in the same family or genus. He also states his opinion that the Piperales are not very primitive, and that, in all probability, their nearest relations are to be found in those cohorts characterized by the presence of perisperm, viz. the Aristolochiales, Polygonales, Centrospermales, and the Ranales.

However this may be, and much may be said against the view here expressed, the facts relating to the structure of the seedlings strongly confirm Johnson's hypothesis[1], and, without expressing an opinion upon the relative primitiveness of the order, the writer is in full accord with this view that *Peperomia* is a reduced genus. And this opinion is, in the case of *Peperomia pellucida*, much strengthened by the fact that 'the embryo remains very small and shows no differentiation when the seed is ripe',[2] which, in the opinion of the present writer, more than counterbalances the increase in the number of the constituent parts in the embryo-sac.

If, then, *Peperomia* be a reduced form, what is the factor which has brought about the reduction?

Both Campbell[3] and Johnson[1] have apparently recognized what Tansley[4] afterwards expressed, viz., that in the apparent absence of some cause to which the reduction may be ascribed, 'the hypotheses of relative primitiveness and of reduction do not stand on an equal footing. The former has the logically prior claim, and must be accepted as a working theory until good grounds can be given for preferring the latter.'

Johnson[5] suggests that the peculiarities of *Peperomia* are analogous to those found in many aquatic, parasitic, and saprophytic Angiosperms; in reply to which, Campbell[6] remarks that 'the habit of the plant in question conforms to neither of these forms, i. e. there is nothing to account for the reduction.'

The present writer suggests that the determining factor which has brought about the reduction may be found in the epiphytic habit of many of the forms.

The second feature of theoretical interest is the bearing of the facts described upon some of the current and possible hypotheses relating to the phylogeny of the Angiosperms. Briefly, these theories are as follows:—

1. The Dicotyledons have arisen from the Gymnosperms.

2. Of the Angiosperms, the Dicotyledons are the more ancient group, and have given origin, through the Ranunculaceae, to Monocotyledons.

3. The Monocotyledons have given rise to the Dicotyledons, the connexion being through the Araceae and the Piperaceae.

4. Further, if it be held that the single seed-leaf has been formed by

[1] Bot. Gaz., xxx, 1900.
[2] Campbell. The Embryo-sac of Peperomia. Ann. Bot., xv, p. 112, 1901.
[3] Loc. cit.
[4] Tansley, A. G. Reduction in Descent. New Phytologist, Vol. i, p. 131, 1902.
[5] Loc. cit. [6] Loc. cit.

the fusion of two cotyledons, then, bearing in mind the resemblances between the Ranunculaceae and certain Monocotyledons, and between the Piperaceae and the Araceae, it may be argued that the Monocotyledons are diphyletic.

We may, with Miss Sargant, consider that the transition phenomena of seedlings have a phylogenetic value; and it is clear that the type of transition herein described is not uncommon in Dicotyledons, so much so, indeed, that Tansley and Thomas[1] remark that 'the importance of this simple and striking type of hypocotyledonary structure is sufficiently apparent from its uniformity in the orders named. The temptation to regard it as of phylogenetic importance in relation to the Dicotyledons as a whole, already strong in view of its occurrence in the almost certainly primitive Ranunculaceae and their allies, is increased by its discovery in the Piperaceae.' This temptation is doubtless strengthened by the occurrence of the type in the Labiatae and Centrospermae. Further, the work of Miss Sargant and Chauveaud shows that a similar type obtains in different orders of the Monocotyledons; Chauveaud[2], in his work on *Pinus maritima*, has described features identical with some of those of this particular type as it occurs in Angiosperms. The differences which obtain may be looked upon as modifications due to the increased number of cotyledons in *Pinus*, and although our knowledge of the seedling anatomy of these plants is decidedly scanty, it is probable that this modified type occurs in other Gymnosperms. Thus the evidence afforded by transition phenomena, if a phylogenetic value be assigned to it, supports all the above contentions. Hence it does not appear, from the facts at our disposal, that this evidence helps in the slightest degree in the elucidation of the phylogeny of the Angiosperms.

But do the transition phenomena yield data of phylogenic importance? Further research will show; in the meantime, it may not be considered inappropriate to draw attention to a few points. Miss Sargant has shown that much variation obtains in this respect in the Liliaceae, a similar diversity has been found by Wright[3] to obtain in different species of Diospyros, the present work shows that the details of the transition in the Piperaceae are anything but rigid, and, finally, the writer has found that there is seemingly much variation in the Centrospermae.

It will probably be agreed that features taken as indicating phylogeny should be sufficiently rigid to withstand the influence of varying conditions, both internal and external.

Is this the case in these transition phenomena?

[1] Loc. cit., p. 106.

[2] Chauveaud, M. G. Passage de la disposition primitive à la disposition secondaire dans les cotylédons du Pin maritime (Pinus maritima). Bull. du Mus. d'Hist. Nat., 1902, No. 7.

[3] Wright, H. The Genus Diospyros in Ceylon; its Morphology, Anatomy and Taxonomy. Ann. Roy. Bot. Gard. Peradeniya, ii, 1904.

Nothing has been said regarding the bearing of the geophilous habit exhibited by certain species of *Peperomia*; we shall be in a better position to discuss this when A. W. Hill[3] has published a detailed account of the highly interesting plants discovered by him in the Andes.

To conclude, it may be stated that this work was commenced in the Jodrell Laboratory, Kew.

I desire to express my thanks to Dr. Scott for placing at my disposal material in his possession, and also to Mr. Hales, Curator of the Old Physic Garden, Chelsea, who not only obtained seeds for me, but also undertook their germination.

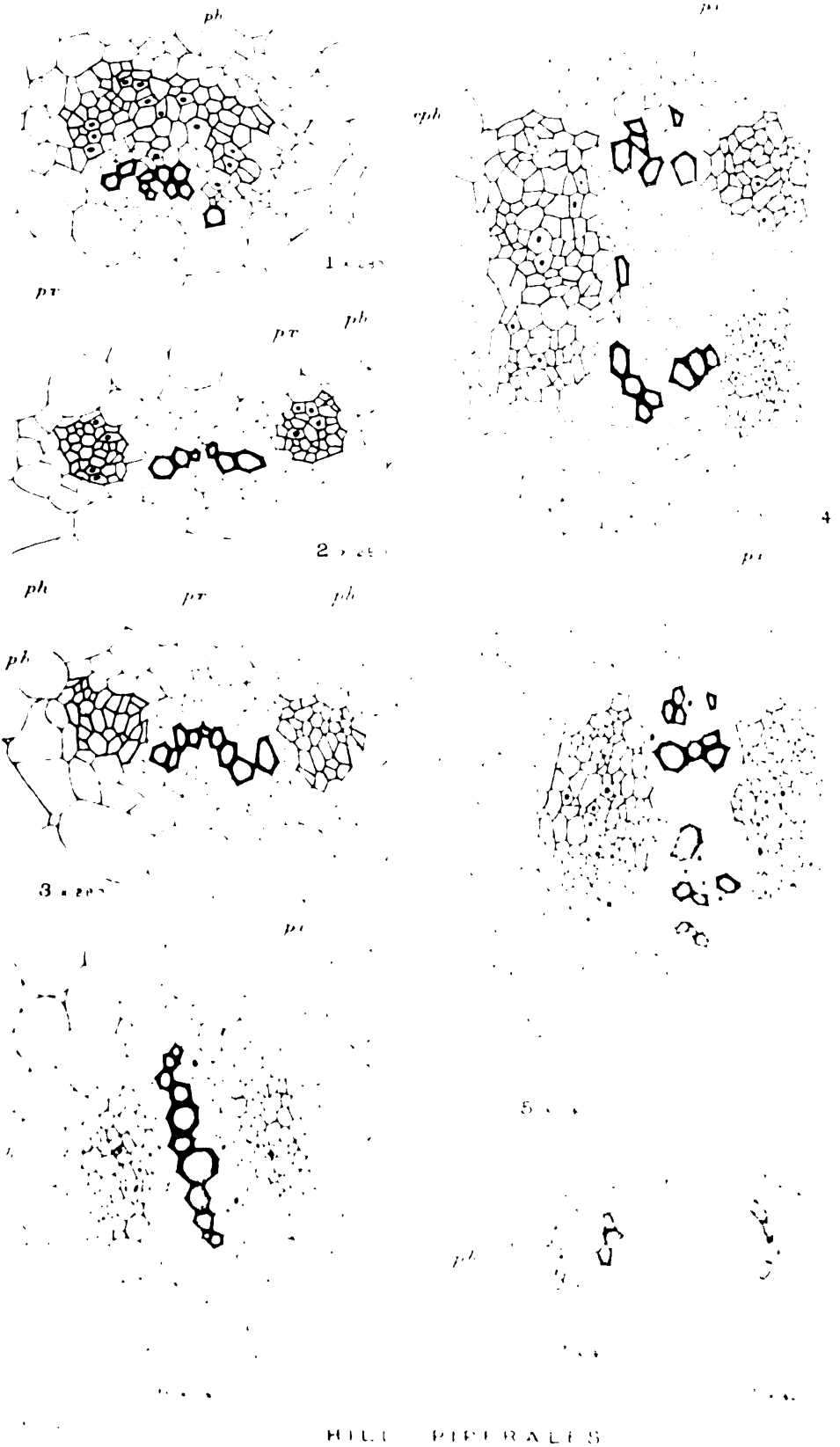
[1] Hill, A. W. Note on some peculiar features in seedlings of Peperomia. Proc. Phil. Soc. Cambridge, Vol. xiii, Pt. i.

EXPLANATION OF PLATE X.

Illustrating Mr. T. G. Hill's paper on the Piperales.

Abbreviations: *c.ph.*, cotyledonary phloem; *cx.*, cotyledonary xylem; *end.*, endodermis; *ph.*, phloem; *px.*, protoxylem; *x.*, xylem; T. S., transverse section.

Fig. 1.	*Piper cornifolium*	T. S. of cotyledonary bundle at the top of the petiole.
Fig. 2.	,, ,,	The same bundle at a lower level.
Fig. 3.	,, ,,	The same immediately before entry into the axis.
Fig. 4.	,, ,,	T. S. hypocotyl before the fusion of the phloem masses.
Fig. 5.	,, ,,	The same after fusion of the phloem groups.
Fig. 6.	,, ,,	T. S. root.
Fig. 7.	*Peperomia eburnea.*	T. S. of one cotyledonary bundle, showing slight bifurcation of the phloem.
Fig. 8.	,, ,,	T. S. of the other cotyledonary bundle, at the same level as in Fig. 7.
Fig. 9.	,, ,,	Same bundle as in Fig. 8, but at a lower level.
Fig. 10.	*Pep. tithymaloides.*	T. S. cotyledonary bundle.
Fig. 11.	,, ,,	T. S. hypocotyl.
Fig. 12.	,, ,,	T. S. root.
Fig. 13.	,, *pellucida.*	T. S. cotyledonary bundle.
Fig. 14.	,, ,,	T. S. hypocotyl.
Fig. 15.	*Houttuynia cordata.*	T. S. cotyledonary bundle.
Fig. 16.	,, ,,	T. S. hypocotyl, showing entry of cotyledon-traces.
Fig. 17.	,, ,,	T. S. root.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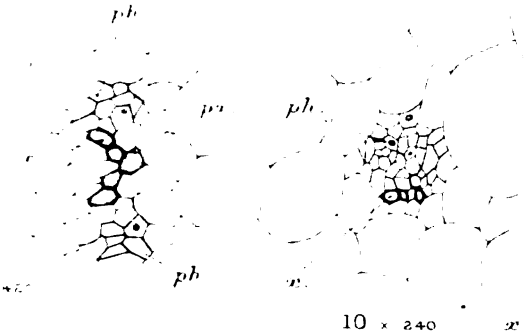

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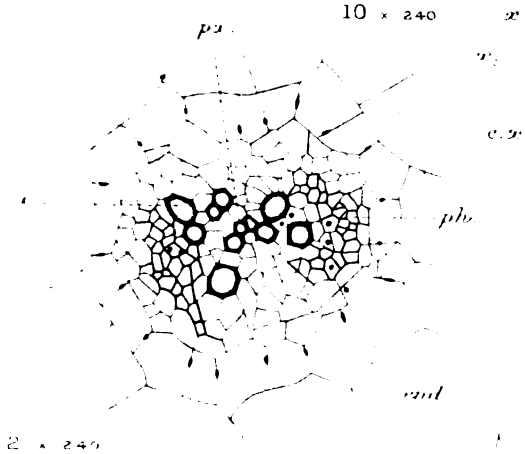

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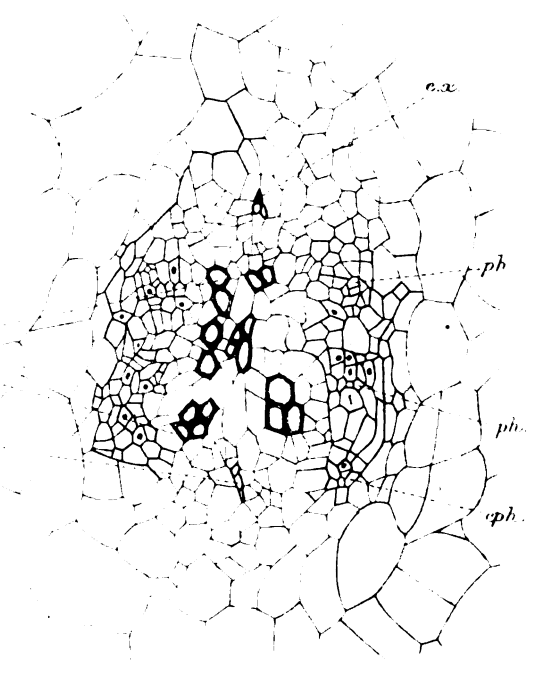

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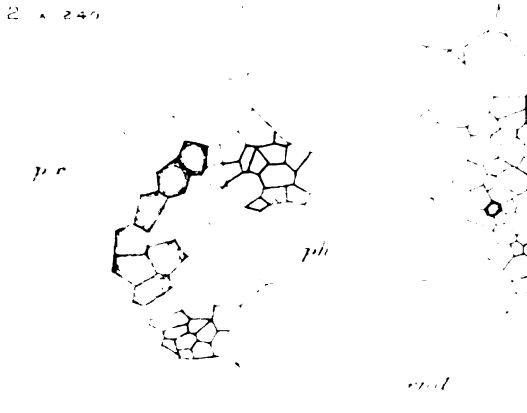

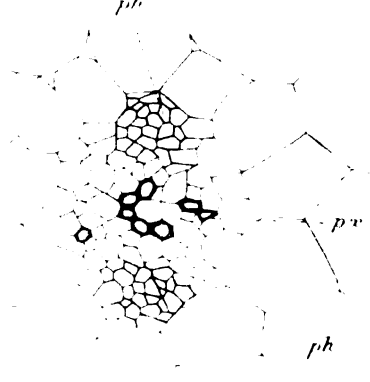

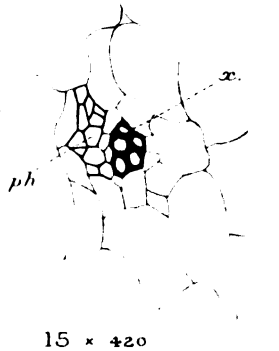

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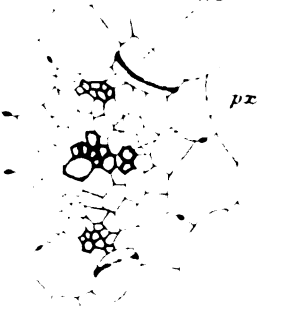

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On the Development of the Spores of Helminthostachys zeylanica.

BY

RUDOLF BEER, B.Sc.

With Plates XI and XII.

THE writings of Goebel [1], Holtzman [2], Campbell [3], and Bower [4] have made us familiar with the early history of the sporangium of the Ophioglossaceae. The actual structure of the spore, however, and the later stages of development, leading up to the establishment of that structure, have, hitherto, only been very imperfectly described for any member of this Order. Recently the publication of two papers, by Cardiff [5] and Stevens [6] respectively, have added considerably to our knowledge of certain stages in the history of the spores of *Botrychium*, but we are still far from having a complete account of even this genus.

Through the kindness of Prof. F. W. Oliver I have had the opportunity of examining a number of fertile spikes of *Helminthostachys zeylanica* which had been preserved in spirit.

Although many important cytological details can only be determined with certainty by the study of material which has been specially fixed for the purpose, it was thought that the following notes might not be without their interest.

The first stages in the development of the sporangium of *Helminthostachys zeylanica* have been followed by Bower, who found the sporangium to be derived from a single superficial cell.

The first periclinal division of the cell defines the sporogenous from the protective portions of the sporangium; 'the sporogenous mass

[1] Goebel, 'Beiträge zur vergleichenden Entwickelungsgeschichte der Sporangien,' Bot. Zeit. 1880, Bd. xxxviii.

[2] Holtzman, 'On the apical growth of the stem and the development of the Sporangium of *Botrychium Virginianum*,' Bot. Gazette, 1892, vol. xvii.

[3] Campbell, 'Mosses and Ferns,' 1895.

[4] Bower, 'Studies in the Morphology of Spore-producing members,' II, 1896.

[5] Cardiff, 'Development of Sporangium in *Botrychium*,' Bot. Gazette, May 1905, vol. xxxix.

[6] Stevens, 'Spore Formation in *Botrychium Virginianum*,' Annals of Botany, October 1905, vol. xix.

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increases rapidly in bulk, whilst the cells surrounding the sporogenous mass, to the extent of several layers, assume the character of a tapetum which gradually becomes disorganised; finally the sporogenous cells separate and the majority of them divide into tetrads; but a considerable portion of them, scattered throughout the sporogenous mass, become disorganised without undergoing division; this is similar to what has been observed in the case of *Ophioglossum*[1].'

My own observations begin with a stage at which the sporogenous cells have reached their full number, but in which the tapetum has not yet become disorganized (Pl. XII, Fig. 15). The tapetal layer is composed of radially elongated cells many of which have divided once or, more rarely, twice by periclinal divisions (Pl. XI, Fig. 1, and Pl. XII, Fig. 15). In *Botrychium* Cardiff observed periclinal divisions to follow one another until the tapetum became four or five cells in thickness. Stevens, however, does not confirm this statement and finds the tapetal layer of *B. virginianum* to be, as a rule, two cells in thickness, which would be more nearly in accordance with what I have seen in *Helminthostachys*.

The membranes of the tapetal cells are delicate, but clearly give the reactions of both cellulose and pectose. In this feature the tapetum of *Helminthostachys* apparently differs from that of *Botrychium*, in which Stevens found each tapetal cell to be 'deliminated by a plasmatic membrane merely.' Although Cardiff does not actually describe the cell-walls of the tapetum, his words certainly imply the occurrence of a cell-wall other than a plasmatic membrane.

The sporogenous cells which lie within the tapetal layer are mostly square or oblong cells which measure about 12–18 μ across (Figs. 16 and 17). Their walls give the characteristic pectic reactions, but neither cellulose nor callose is to be found in them. The cytoplasm of these cells is fairly dense and contains a number of plastids usually crowded with starch. In slightly older sporangia the tapetal walls begin to break down, and in these disorganizing membranes I no longer succeeded in obtaining the cellulose reactions, although pectose was still clearly demonstrable[2].

The cytoplasm derived from the disorganized cells flows together (Figs. 2 and 16) and increases in amount, whilst the nuclei, which are mostly gathered together in little nests or groups at the inner or outer periphery of the tapetal layer, have become more numerous. The groups of nuclei are no doubt partly formed by the approximation of nuclei from several disorganized cells, but there can be little doubt that they also represent, to some extent, a number of daughter-nuclei which have origin-

[1] Spore-producing members, Part II, 1896, p. 35.

[2] I state this fact for what it is worth, although the failure of the cellulose reactions may be due to the increased difficulty of demonstration rather than to the real absence of this substance.

ated from the amitotic division of one or more mother-nuclei. The occurrence of constricted nuclei, such as I have represented in Fig. 2, bears out this view. Neither here, nor at any subsequent stage, have I seen tapetal nuclei dividing by mitosis.

The tapetal cytoplasm at this stage contains a quantity of starch and, in iron-haematoxylin-bismarck-brown preparations, presents a finely vacuolated appearance.

Up to the present the sporogenous cells have been united together in one coherent mass, but now they show the first signs of separating from one another (Fig. 17). The separation takes place in 'blocks' quite comparable with those described by Cardiff in *Botrychium*[1]. In *Helminthostachys*, as in *Botrychium*, the separation appears to take place approximately 'in the order in which the original walls were laid down in the archesporium and young sporogenous mass.' The nuclei of the sporogenous cells of *Helminthostachys* are still in the resting condition when the separation of the 'blocks' commences.

Delicate and undifferentiated as the walls of the sporogenous cells appear, they must nevertheless possess a greater complexity of structure than becomes apparent with our instruments, for during the process of the separation of the sporogenous cells from one another a middle lamella becomes mucilaginous and is finally dissolved, whilst a secondary thickening layer remains unaltered round each sporogenous cell. The entire sporogenous membrane, both before and after the mucilaginous alteration of the middle lamella, gives no other reactions than those of pectic bodies. If I understand Stevens correctly, he found the mother-cells of *Botrychium* to be demarcated from one another and from the tapetum by a delicate plasmatic membrane alone, but Cardiff's statements do not bear this out and it certainly does not apply to the mother-cells of *Helminthostachys*. The sporogenous cells now divide into the spore-tetrads.

In the first division of the spore-mother-cells the chromosomes (which presumably occur in the reduced number) are seen to be small in size and rather crowded upon the spindle (Fig. 3). I have not succeeded in accurately counting their number, but I should very roughly estimate this to be between forty and sixty. Stevens has not recorded the number of chromosomes which occur in *Botrychium*. The spindle was surprisingly well preserved in the alcohol material and could be seen to terminate in very sharp, almost acuminate apices at which no traces of centrosomes were ever observed. The spindle extends to the very periphery of the mother-cell and is free from any radiations at its poles (Fig. 4). The daughter-nuclei, resulting from the first division, have in some of my preparations a curiously flattened, almost hemispherical shape when viewed in profile[2] (Fig. 5). They appear, like those of *Botrychium*, to enter into a resting

[1] Cardiff, l. c., p. 342.

[2] Compare this with Stevens' Plate XXIX, Fig. 28.

stage before passing on to the second division. The spore-mother-cells do not divide simultaneously, but all stages of division can be found in one sporangium. A mother-cell with its nucleus in the prophases of the first division not uncommonly occurs side by side with one which has completed its second division and has already developed the tetrad- (special-mother-cell) walls. In *Botrychium* Cardiff found that the cells in the same 'block' are always in the same stage, but in *Helminthostachys* the separation of the mother-cells has, apparently, been more complete before they enter upon the maiotic divisions, so that they have reached greater independence from one another than is the case in *Botrychium*.

Bower found that a considerable proportion of sporogenous cells became disorganized without undergoing division. In *Botrychium* Cardiff found no such disorganization to occur, and my preparations of *Helminthostachys* are quite in accordance with his observations and show no abortion of mother-cells. When the two divisions of the mother-cell have been completed the four cells of the tetrad are enveloped by the tetrad-wall (special-mother-cell wall) (Fig. 18).

This membrane is very delicate and in this respect forms a striking contrast to the conspicuous tetrad-walls of nearly all the other plants that I have examined (e.g. *Riccia*, *Anthoceros*, Lycopodiaceae, *Osmunda* &c.). It gives the pectic reactions very clearly, whilst several times I obtained a rather faint violet-pink reaction with calcium-chloride-iodine solution. For some unexplained reason the calcium-chloride-iodine solution does not always produce the same result; the tetrad-wall in some cases colouring violet-pink, in others yellow.

While we may, therefore, conclude with certainty that this wall contains pectose, we must leave it undecided whether or not this substance is accompanied by cellulose[1]. The young spore-membrane colours, although rather faintly, with bismarck-brown, methylene blue, and similar dyes, and appears to be more or less cuticularized from a very early stage. It is a new formation and is not derived from the transformation of the special-mother-cell wall, which can still be recognized outside the spore-membrane (Fig. 6). In the meanwhile the disorganization of the tapetal walls has become complete, whilst the tapetal cytoplasm, which now forms a sort of plasmodium around the sporogenous cells (Fig. 16), has increased considerably in amount. The numerous nuclei which it contains still tend to be aggregated in groups.

We now find the plasmodial envelope sending finger-like processes into the cavity of the sporangium between the separated sporogenous cells. These cytoplasmic processes spread further and further between the sporogenous cells, branching and anastomosing with one another and separating

[1] No other cellulose reaction, but only the inconstant appearance of the violet-pink colour with calcium-chloride-iodine, was given by these walls.

the young tetrads more and more completely from one another (Fig. 18). At first these plasmodial strands consist solely of cytoplasm, unaccompanied by nuclei, which remain in the peripheral envelope. Soon, however, we can observe the nuclei dipping into the broader arms of cytoplasm and making their way into the interior of the sporangial cavity. As the round or oval nucleus passes into the strand of cytoplasm it usually alters its shape and becomes drawn-out, often into a very fine point, at its anterior extremity (Fig. 7). It usually stains more deeply at this beak-like process than it does at its blunt, posterior end. As it moves further along the strand and passes between the spore-tetrads it not infrequently assumes an elongated form, sometimes almost justifying the term vermiform, until it temporarily comes to rest at this or that spot, when it reassumes a more iso-diametric shape. The tapetal plasma, which has a finely vacuolated structure in successful preparations, contains an abundant supply of starch. All the cells composing the walls of the sporangium are rich in starch; the membranes of these cells give the pectic and cellulose reactions. The spores remain associated together in groups of four throughout the greater part of their development. They now rapidly increase in size, but their walls remain very thin and the cytoplasm they enclose is scanty. In consequence of this the spores, at this stage, are nearly all collapsed in the alcohol material (Fig. 19). The young spores are tetrahedral in shape and the edges of those surfaces which adjoin one another in the neighbouring spores of a tetrad are raised up into ridges. In this way each spore develops three ridges upon its surface, and these ridges converge to a common point (Fig. 8, *a*).

Early in the history of the spore one can see that the sides of the tetrahedron which meet at the ridges are only very loosely joined together. The action of various reagents, and even the pressure of the microtome knife, often leaves the spore with three flaps entirely separated from one another at the ridges, as is shown in Fig. 8, *b*. The cuticularized wall of the spore now grows somewhat in thickness, and at about this time a new layer—the endospore—makes its appearance within it. This layer, which gives the reactions of a pectic body, can be traced as a continuous, although delicate, layer over the entire inner surface of the spore-wall.

In microtome sections which have passed through the apex [1] of the spore we can trace a little process or fold of the endospore which has pushed between the ridges of the exospore and which reaches to the outer surface (Fig. 9). In spores measuring about 23 μ across their longest diameter the exospore has become sufficiently thick to prevent the collapse of the spore in alcohol. The surface of the spore is still smooth and its protoplast poor in substance [2].

[1] Viz., the point at which the three ridges meet.

[2] It usually contains a very little starch, however.

The further growth in thickness of the exospore continues to leave the fold of endospore uncovered at the apex of the spore. The smooth surface of the exospore now becomes slightly wavy in outline, and this soon leads to the formation of the reticular sculpture which is characteristic of the mature spore.

The fully grown spore measures, in section, about 33 μ by 28 μ. The exospore is thicker at the apex than over the rest of the spore, but is perforated by a cleft through which the fold of endospore reaches the exterior. This cleft is particularly well seen after treatment with a mixture of sulphuric and chromic acids or with sulphuric acid alone, but it can be quite readily distinguished in sections which have been stained with methylene blue, or bismarck-brown without the previous action of acid. Chlor.-zinc-iodine solution, to which more iodine than usual has been added, also very clearly shows the endospore—coloured brown—penetrating the exospore and reaching the exterior. The reticular sculpturing upon the surface of the exospore appears in section as a series of blunt processes with flattened summits (Figs. 10 and 11). The protoplast of the spore has now become somewhat richer in substance and usually includes starch, but not in any quantity.

Nothing in the nature of an epispore is to be found in the spores of *Helminthostachys*. The exospore and, most probably, also the endospore are in the first place deposited by the secretory activity of the spore-protoplast. There is no possibility of the former layer being derived from the transformation of part or all of the mother-cell-wall, since this at all times very delicate wall can still be distinguished, in apparently undiminished thickness, over the surface of the young exospore (Fig. 6).

The fact that the exospore and endospore are inseparably united together at first suggests the probability of the two layers being derived from the differentiation of an originally single, homogeneous membrane. As Fitting[1] has already pointed out, however, the existence of a close fusion between two layers of a wall does not necessarily indicate their common origin by differentiation, and there are several well-known cases in which two lamellae are intimately bound together, but which unquestionably have been separately deposited by the cell-protoplast. In the present instance, moreover, it is difficult to understand how a cuticularized membrane can be so differentiated as to give rise to a pure pectic lamella on one of its faces. The development of the little fold of endospore at the apex of the spore is also more readily explained as a new formation than as a product of differentiation. Shortly after the exospore has been formed round the young spore and throughout the time that this layer is growing in thickness and in surface the tapetal plasmodium which envelops the spore-tetrads shows unmistakable signs of metabolic activity.

[1] H. Fitting, Bot. Zeitung, Bd. lviii, 1900, p. 126.

It is impossible to escape the conclusion that this metabolism is concerned with the elaboration of material for the growth of the exospore. That such material must be forthcoming is of course obvious, and the two sources to which one naturally looks for this supply are the spore-protoplast on the one hand and the tapetum upon the other. In *Helminthostachys* (at least in my spirit material) the spore protoplast, after the first formation of the exospore, is very poor in substance, and it is very unlikely that it can furnish sufficient plastic material for the growth of the wall. When one turns to the tapetum, however, one finds here a gradual utilization of reserve-materials which can fully account for the substance which is being employed in the growth of the exospore. Moreover, if we deny that the tapetal material is being utilized for this purpose it is not easy to see what the fate of this substance may be. The growth of the wall of the sporangium is amply provided for by the reserve-materials contained in its cells, whilst the protoplasts of the spores do not increase in size or substance during this time, so that we are driven to associate the disappearance of starch and cytoplasm from the tapetum with the only other demonstrable utilization of material, viz., that which is adding to the size and thickness of the spore-coats.

It is impossible at present, however, to decide whether the material elaborated in the tapetum is directly built up in the spore-walls or whether it first passes, in a liquid form, into the spore-protoplast which, either with or without further elaboration, distributes it to the walls.

In view of the important part that the tapetal plasmodium plays in the growth of the spore-walls it will be necessary at this point to look more closely at its appearance and behaviour. We find that starch is abundant in the tapetal cytoplasm before the walls of the tapetum disorganize and that it continues to exist there in considerable quantities until the period during which the exospore undergoes its most active growth in thickness. During this time the tapetal plasma is either very poor in starch or, more often, this substance is quite absent from it. When the exospore has completed its growth in thickness and the spore-protoplast is about to add to its substance, starch can usually again be seen in the tapetal cytoplasm but never in quantities that can compare with those which occurred in the early stages of sporangial development.

The tapetal cytoplasm at first increases somewhat in amount (immediately after the disorganization of the tapetal cells), but during the later history of development it slowly but steadily decreases in quantity (compare Figs. 18, 19, and 20). Where it abuts upon a vacuole (such as that which encloses a spore or spore-tetrad) the cytoplast has a very clearly marked plasmatic membrane; elsewhere it is finely vacuolated in structure. It is the vacuolar cytoplasm which is gradually utilized in the metabolic processes of the plasmodium, and the plasmatic membranes,

which limit neighbouring vacuoles in consequence approach one another more and more closely. In sporangia, shortly before their dehiscence, the vacuolar cytoplasm has almost completely disappeared, but the plasmatic membranes are still present between the spores (Fig. 20). These can then, in nearly all cases, be seen to be double in structure owing to the complete approximation of the plasmatic membrane of adjoining vacuoles[1]. Starch grains can not infrequently be seen flattened out between the two adpressed membranes and, at the angles formed by the meeting of several vacuoles, nuclei occur.

The nuclei show, at all stages, considerable variation in size, in form, and in character. In *Botrychium* Cardiff found that the nuclei underwent a very considerable increase in size during development; thus in young sporangia he gives their size as 8 μ, whilst at a later stage he found them to measure 15–20 μ. In *Helminthostachys* the general average of size of the tapetal nuclei appears to remain about the same at different periods of development.

(*a*) *Tapetal cells still intact* . . . . . = 13 × 11 μ
(*b*) *Young spores with thin, smooth exospore* . . = 13·4 × 10 μ
(*c*) *Spores with immature sculpturing on exospore* . = 12·6 × 9·6 μ
(*d*) *Spores just before dehiscence of sporangium* . = 13 × 11 μ.

The above figures are the averages calculated from a large number of countings and they show practically no alteration in the size of the tapetal nuclei.

The form of the nuclei is very various. In the tapetal cells before disorganization and in the tapetal plasmodium before this flows between the sporogenous cells the nuclei are more or less oval in shape. The peculiar alteration in form which they often undergo as they pass within the sporangial cavity has already been described. In the later periods of development these nuclei are sometimes oval or spherical in outline; often they are irregular in shape and occasionally their form is angular (Fig. 12). They possess, in most cases, a distinct nuclear membrane and are usually rich in chromatin; several nucleoli can generally be seen in each nucleus. The chromatic granules are often closely packed (and the nucleus in consequence deep-staining) in the smaller nuclei, whilst in the larger nuclei the chromatin-grains are frequently separated more widely from one another and the nucleus contains more non-staining material.

In *Botrychium* Cardiff found that 'as the spores commence to separate in the tetrad, the tapetal cytoplasm has entirely filled the sporangium and many of the nuclei have begun to disorganize, though they seem unusually persistent and many are found after the tetrad is fully formed. Later,

[1] In consequence of the entire disappearance of the vacuolar cytoplasm which separated them from one another at an earlier stage.

when the spores are entirely separated and mature, the tapetum disappears.' In *Helminthostachys* the tapetum and tapetal nuclei are evidently more persistent than Cardiff found to be the case in *Botrychium*[1]. It has already been mentioned that the plasmatic membranes and many nuclei are still to be found between spores which are quite or nearly mature, and I have rarely found nuclei which were degenerating except in sporangia which were almost ready to dehisce. In such sporangia the majority of the nuclei stained intensely and were closely packed with chromatic granules, whilst here and there a nucleus was seen in which the nuclear membrane had disappeared and the granules were becoming dispersed (Fig. 13). Mitotic divisions of the tapetal nuclei were at no time seen.

Cardiff records frequent amitotic divisions of the tapetal nuclei of *Botrychium*, but Stevens was unable to confirm this observation.

In *Helminthostachys* I have found reason to believe that in the early stages of sporangial development, immediately after the tapetal membranes have disintegrated, the nuclei do multiply by direct division, but in older sporangia it is much more difficult to find any evidence of such divisions. Irregularities in outline, which sometimes lead to a more or less constricted shape, not uncommonly occur, but most of these are undoubtedly to be referred to those passing changes of form which are so frequently to be found in nuclei that are taking part in active metabolic processes. Occasionally these changes of form may actually lead to a division of the nucleus, but in my material this is certainly rare. An isolated instance of such a division is shown in Fig. 14. Very possibly the conditions which prevail at the time when the material is collected may exert an influence upon the tapetal nuclei and may explain the differences which occur in the accounts of Cardiff and Stevens.

The principal features, therefore, which the tapetal plasmodium presents during the period of exospore growth are (*a*) an almost or quite complete disappearance of starch, (*b*) a gradual diminution of the finely vacuolar cytoplasm, and (*c*) the richly chromatic nuclei which often show irregularities of outline.

These features, I think, bear out the view already expressed that the tapetal plasmodium is the centre of metabolic activities in which a substance is elaborated from the raw materials contained in the tapetum. For reasons already stated we may further conclude that this substance is, directly or indirectly, employed in the growth of the spore-wall.

[1] Stevens also records much greater persistence of the nuclei in the *Botrychium* examined by him.

EXPLANATION OF PLATES XI AND XII

Illustrating Mr. Beer's paper on the Spores of *Helminthostachys*.

PLATE XI. DRAWINGS.

Fig. 1. Tapetal cells. × 660.

Fig. 2. Nest of nuclei lying at the inner periphery of the disintegrating tapetum. *a*, a constricted nucleus which is probably dividing amitotically. × 850.

Fig. 3. Chromosomes during first division of the spore-mother-cell. × 1100.

Fig. 4. Spindle and chromosomes during first division of the spore-mother-cell. × 850.

Fig. 5. Daughter-nuclei resulting from first division of the spore-mother-cell. × 1100.

Fig. 6. Tetrad showing the very young spore-wall (left white) surrounded by the special-mother-cell wall (drawn black). × 850.

Fig. 7. Tapetal plasmodium. Nuclei passing into one of the cytoplasmic strands which reach into the interior of the sporangium. × 850.

Fig. 8, *a* and *b*. Young spores. In *b* the wall has separated into three flaps at the ridges. × 850.

Fig. 9. Apex of young spore; showing little fold of endospore in section. × 850.

Figs. 10 and 11. Nearly mature spores. Fig. 10 looked at from above; Fig. 11 in section. Both × 850.

Fig. 12. Tapetal nuclei from a sporangium in which spores had thickened, but still smooth exospores. × 850.

Fig. 13. Nuclei from tapetum of mature sporangium.

Fig. 14. Nucleus from tapetal plasmodium of a sporangium in which the young spores were surrounded by a thin exospore. Amitosis (?) × 850.

PLATE XII. PHOTOGRAPHS.

Fig. 15. Young sporangium; tapetal cells surrounding the spore-mother-cells. The break in the mass of mother-cells is caused in preparing the section and does not indicate a natural separation of these.

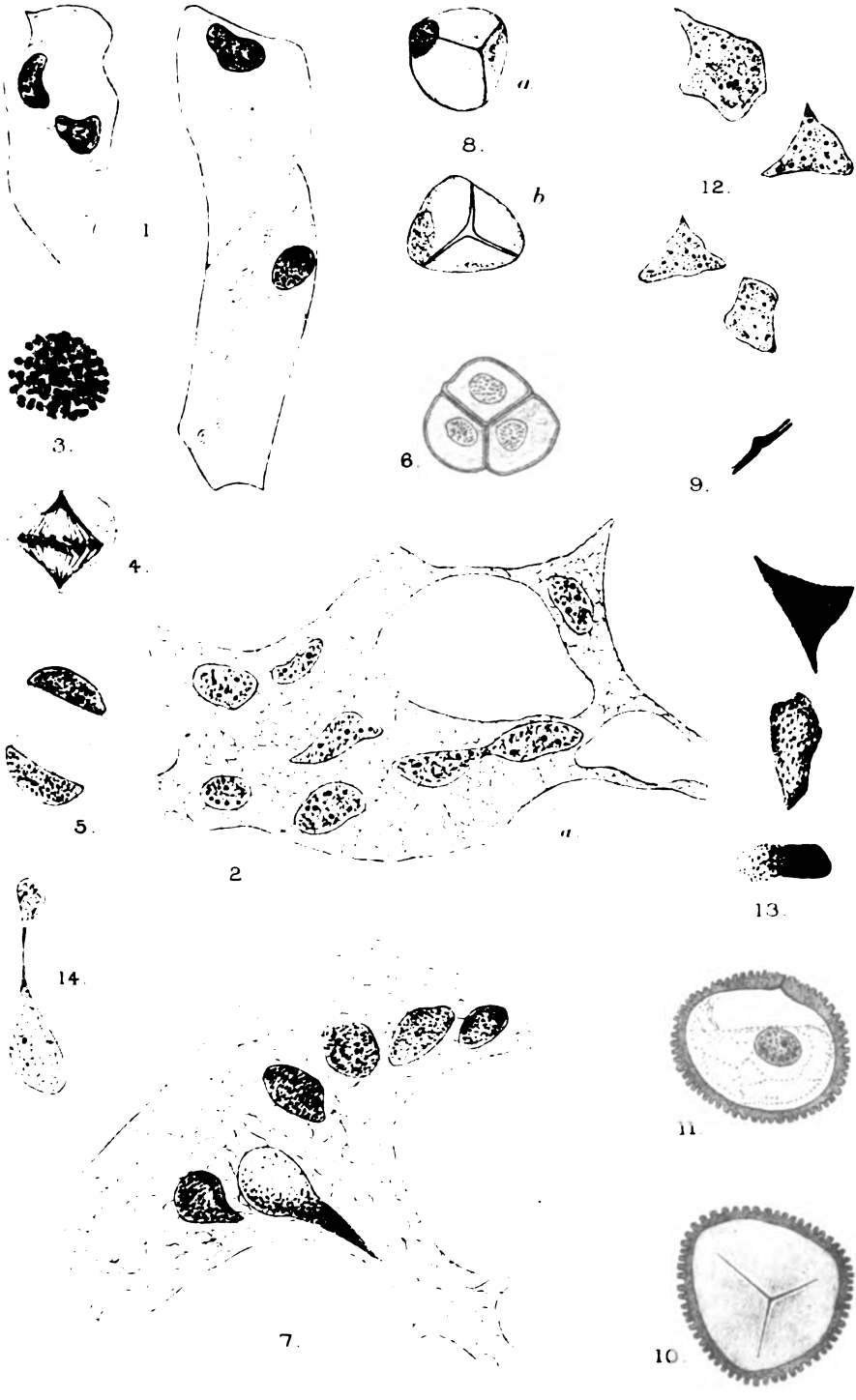
Fig. 16. Spore-mother-cells surrounded by the tapetal plasmodium. The tapetal membranes have all disintegrated.

Fig. 17. Early stage in the separation of the spore-mother-cells from one another. The first lines of the mucilaginous degeneration of the middle lamellae are shown.

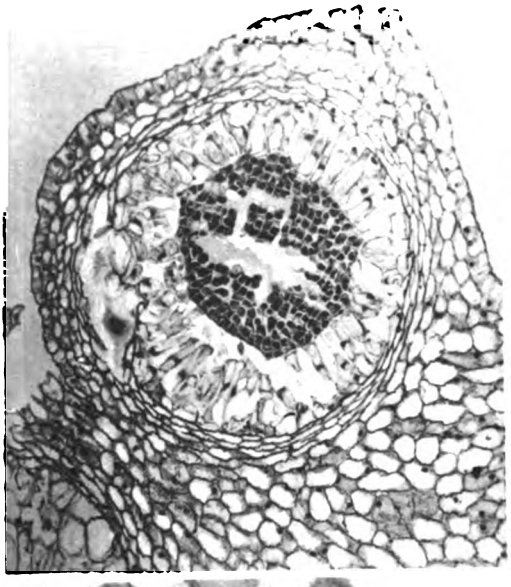
Fig. 18. The young tetrads (special-mother-cells) with tapetal plasmodium gradually flowing between them.

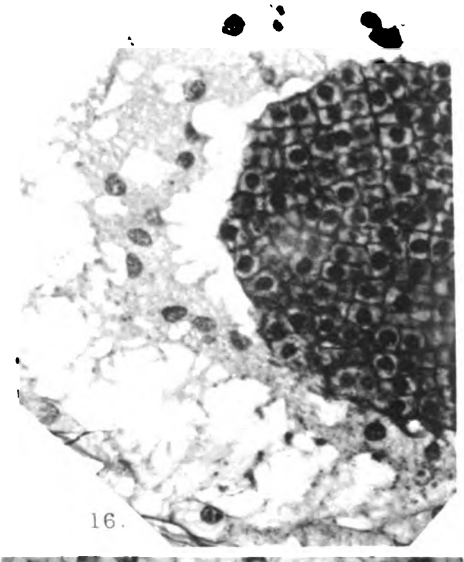
Fig. 19. Older stage, showing distribution of tapetal plasmodium between the spore-tetrads. The young spores have all collapsed in the alcohol.

Fig. 20. Almost mature spores. The plasmatic membranes of the tapetal plasma still surround the spores. The spores to the extreme right of the figure show the little fold of endospore penetrating the cleft in the apex of the exospore.



BEER – HELMINTHOSTACHYS.





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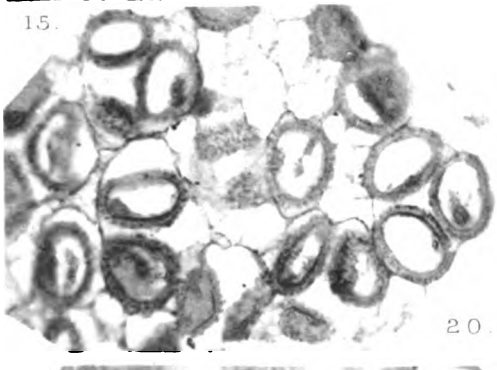

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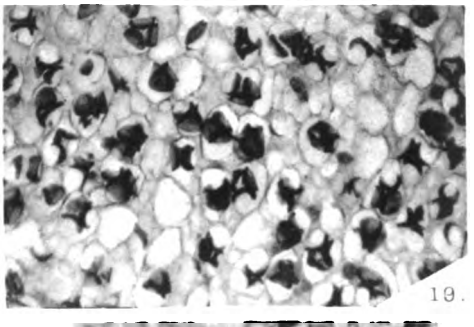

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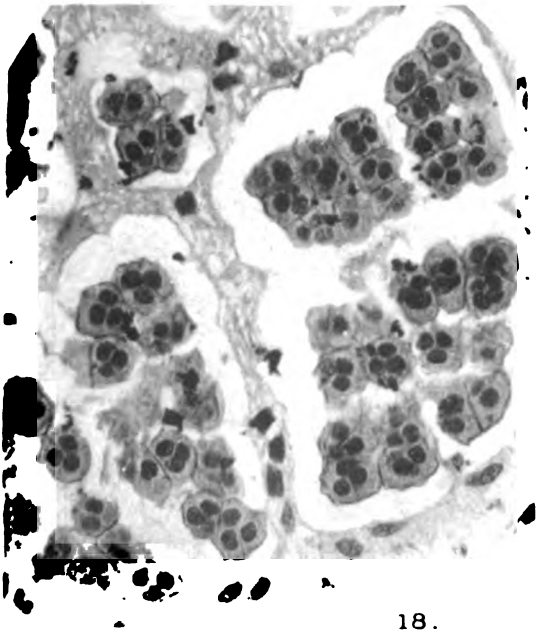

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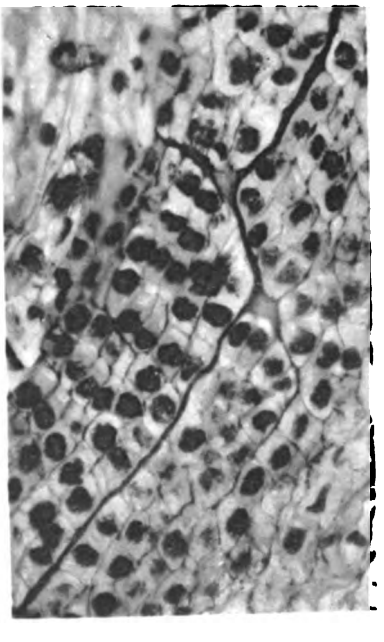

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Huth coll

BEER— HELMINTHOSTACHYS.

On Oidiopsis taurica (Lév.), an endophytic member of the Erysiphaceae [1].

BY

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With Plates XIII and XIV.

IN a preliminary note published (1) at the beginning of last year, I called attention to the fact that *Erysiphe taurica* Lév. is endophytic in its conidial stage, the conidiophores being sent through the stomatal apertures into the open air from intercellular hyphae in the mesophyll of the leaf, instead of arising from a superficial mycelium on the surface of the leaf, as in all hitherto known species of the Erysiphaceae. Further, the conidiophore is frequently found to be branched, a character not previously known to occur in the Family.

During the past year I have examined a large number of specimens of *E. taurica* in the conidial and perithecial stages [2], and I propose now to give the results of this examination, and also to make some observations on the life-history of *E. taurica*, and on the systematic position of the species. It may be mentioned here that one result of the examination of the collected material has been the establishment of the identity of several recently published fungi with *E. taurica*.

In the early stages of the conidial condition *E. taurica* in no way resembles the other species of the Erysiphaceae. This is due to two peculiarities, viz. the complete absence at this stage of any mycelium on the surface of the leaf, and the presence of conidiophores emerging singly or in bundles through the stomatal apertures (see Figs. 5–7, 12, 13, 17). The conidiophore is thin-walled, septate, flaccid, 200 to 700 μ, or more, in length, sometimes simple [3], but more often branched. The branching is

[1] From the Jodrell Laboratory, Royal Botanic Gardens, Kew.

[2] All the material mentioned in the present paper is deposited in the Kew Herbarium.

[3] It is possible that the simple conidiophore becomes branched at a later stage through the production of lateral branches. In the example shown in Fig. 6 the lateral branches evidently arose at a late stage in the growth of the conidiophore, as shown by the fact that the walls of the main axis are comparatively thick, while the walls of the developing lateral branch are very thin (see *x*, *x*). Compare also Fig. 13.

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sometimes monopodial (and repeated in the branches of the first and second order) and more or less definite; at other times it is apparently quite indefinite. From certain cases observed, it appears that mycelial hyphae may grow out from the conidiophore. The conidia are borne singly at the apices of the main axis and lateral branches. It appears, from certain dried examples which I have seen, that after the first conidium has been abstricted another may sometimes be produced [1]. In this character the present fungus resembles *Phyllactinia* (see (5), p. 494). The conidium is extremely variable in size and shape, even when taken from the same host-plant, as can be seen by referring to the figures in Plates XIII and XIV. On some hosts, however, the conidium shows constant and distinctive characters as regards its shape. The variations shown by the conidium in examples of the species on different host-plants will be dealt with fully below.

As mentioned above, the mycelium is at first wholly internal. The endophytic hyphae are abundant just below the epidermis, where they run freely in the intercellular spaces, and often form a kind of thin weft. Besides winding in and out among the intercellular spaces between the cells of the spongy parenchyma, the hyphae not infrequently extend to the intercellular spaces between the cells of the palisade tissue. In those cases where stomata are frequent on both surfaces of the leaves, the intercellular mycelium runs throughout the intercellular spaces of the mesophyll, and sends out the conidiophores and the hyphae of the external mycelium through the stomata of both surfaces to an equal extent. The hyphae of the endophytic mycelium are septate, from 4 to 6 μ in diameter, and are sometimes tortuous and branched, with numerous free ends, while they sometimes run nearly straight for considerable distances in the intercellular spaces just below the epidermis (Fig. 3). Often mesophyll cells, here and there, become closely invested by a weft of hyphae. From the intercellular hyphae small haustoria, more or less globular in shape, are sent into the mesophyll cells, both those of the spongy parenchyma and frequently also those of the palisade tissue. I have not observed any cases in which the epidermal cell has been entered for the production of a haustorium by penetration of the inner wall.

In the later stages of the conidial condition, the fungus becomes more evident on the surface of the host-plant, and approaches in habit the other members of the Erysiphaceae, because mycelial hyphae now emerge in

[1] The statements of authors with regard to this point have been as follows. Sorokine (in Revue mycolog., 1889, p. 146), speaking of *Erysiphe Saxaouli* [= *E. taurica*], says, 'Il n'y a qu'une seule spore sur chaque hyphe verticale.' Scalia writes of *Oidiopsis sicula*, 'conidiis catenulatis, facillime secedentibus,' and states that when the conidiophore is branched 'a chain of conidia, in the manner of *Oidium*, is produced on each branch.' The same author in his diagnosis of *Oidium gigasporum* says, 'conidiis catenulatis,' and also, 'the conidia become abstricted directly they are formed.' Maire observes, 'Les conidiophores donnent naissance à leur sommet à un petit nombre de conidies qui se forment et se désarticulent successivement; quelquefois il ne se forme qu'une seule conidie.'

great numbers through the stomata, and form an external mycelium (varying in consistence from arachnoid to felted tomentose) on the surface of the leaf or stem preparatory to the formation of perithecia. In some cases it appears that some of the hyphae which form this external mycelium may arise as lateral branches from the conidiophores [1]. The hyphae of the external mycelium, in many cases if not in all, nourish themselves by sending down branches through the stomata, exactly as in the case of the hemi-endophytic mycelium of *Phyllactinia* (see Palla (11); also Monograph (2), p. 4, fig. 163). So far as I have been able to observe from the herbarium material available, no haustoria are sent by the external hyphae through the cuticle into the epidermal cells. Nevertheless the hyphae which creep on the surface of the leaf during the latter part of the conidial stage, and throughout the perithecial stage, possess peculiarly shaped short lateral branches, which in some cases are very similar to the appressoria on the hyphae of ectoparasitic species. These short lateral branches, which are figured in Plate XIII, Figs. 4, 20, 21, are often closely applied to the surface of the epidermis, and appear to serve the purpose of attaching the hyphae to the leaf; in the herbarium material available I have not been able to observe that haustoria are ever produced from these appressoria. It may be noted here, as a fact of considerable interest, that the mycelial hyphae of the hemi-endophytic species *Phyllactinia corylea* possess appressoria of exactly similar shape, and in this species also no haustoria are sent into the epidermal cells from these organs.

I have been able to observe the early stages of germination of the conidium. Living examples of the fungus, in the conidial stage only, occurring on *Ballota rupestris* [2], were kindly sent to me from Sicily by Prof. G. Scalia. As, unfortunately, plants of *B. rupestris* were not available for inoculation experiments, I used the leaves of *Eryngium campestre*, one of the host-plants of *E. taurica*. The leaves which were inoculated were treated as follows: At the place of inoculation the upper epidermis and most of the underlying mesophyll tissue were cut away, leaving the under epidermis intact. Conidia were sown on the cuticular surface of the uninjured epidermal cells over the wound, and the leaf placed, with the cut surface downwards, on damp blotting-paper at the bottom of a closed Petri dish. The stages of germination reached by the conidia are shown in Fig. 10. It is an interesting fact that the conidium on germination at once forms an appressorium, just as is the case with the germinating conidia of the ecto-

[1] This accords with the observations made by Maire (6) in his paper referred to later. This author remarks, writing of the superficial mycelium: 'Il est formé de tubes beaucoup plus fins que le mycélium interne. Ces tubes prennent naissance par ramification latérale des conidiophores près de leur base, ou plus haut, ou encore aux dépens de filaments spéciaux, sortant des stomates en même temps que les conidiophores.'

[2] This is the form which has been described as *Oidium gigasporum* (see below, p. 190).

parasitic species [1]. No formation of a haustorium from this appressorium was observed, nor was the germ-tube seen to enter a stoma; as, however, these conidia had been sown on an injured leaf of a strange host-plant as regards the form of the fungus used, these negative results are of little importance.

The identity of four recently published species with *E. taurica* may here be pointed out.

In 1900 Magnus published (7), as a new species, *Oidium Haplophylli*, occurring on *Ruta* (*Haplophyllum*) *Buxbaumii*, in Palestine. Through the kindness of Prof. P. Magnus I have been able to examine the type specimens of this fungus, and have found the endophytic mycelium, the branched conidiophores emerging through the stomata of the leaf, and the large, curiously shaped conidia characteristic of *E. taurica*.

In 1902 Scalia described (9), (10), as a new genus of the *Hyphomycetes*, a fungus occurring on *Asclepias curassavica* in Sicily. A careful and very interesting description of the fungus, to which the author gave the name of *Oidiopsis sicula*, was published (l. c.), and I give below (in translation) the more important biological observations there recorded: 'The fungus forms on the upper surface of the leaves purple spots, which are more or less extended and always limited by the midrib and its branches. Corresponding to these spots, one observes on the lower surface a kind of white mealy tomentum, which at first sight makes one doubt whether one is not dealing with a *Peronospora*. The injury caused is entirely comparable to that brought about by species of *Peronospora*. The leaf dries up very quickly, either locally at the isolated spots, or the whole lamina withers if the spots become confluent, so as to cover its surface. The plants become rather easily defoliated, and flower badly. In gardens in Sicily the fungus lives all the year on *A. curassavica*; in the summer months the spots are not observable on the upper surface of the leaf. Plants cultivated in damp and shady localities are injured most. The maximum of infection takes place during the winter, and chiefly if the season is mild. The fungus develops less actively during the summer months; unless there are prolonged rains, or even simply damp winds.'

At the same time Scalia published (10, p. 9) a fungus occurring on *Ballota rupestris*, in Sicily, as a new species of *Oidium*, under the name of *Oidium gigasporum*. In the description the following characters are given: 'The fungus appears as coloured spots on the upper surface of the leaves, on the lower surface and corresponding to these spots one observes a white mealy pruinose layer, somewhat clearly visible among the hairs with which the leaf is abundantly provided. The mycelium is composed of creeping hyphae which are branched and hyaline, and form

[1] The figure to the right represents a conidium twenty-four hours after being sown; that to the left, after forty-eight hours. On the sixth day the germ-tube was considerably longer, and passing several stomata (which, however, were not functional) had developed two more 'appressoria.'

a rather delicate arachnoid weft. From the sterile hyphae arise the conidiophores, which are for the most part simple, though sometimes at their base a secondary branch is developed. The conidia, formed at the apex of these conidiophores, become abstricted directly they are formed. Of these conidia, the terminal one is usually attenuated at the apex and truncate at the base, while the others are cylindrical and rounded at both ends, and roughly oval. This species is absolutely distinct from the other species of the genus [*Oidium*] in the much greater dimensions of the conidia, as well as in the host-plant on which it lives; it is, however, very like the following species [*Oidiopsis sicula*] in almost all its characters, although the mycelium in the present species is superficial, as in typical species of *Oidium*, while in *Oidiopsis sicula* it is endophytic.'

Through the courtesy of Prof. G. Scalia I have been able to examine excellent dried examples of *Oidiopsis sicula* and *Oidium gigasporum*, and also spirit material of the former. There is no doubt that both belong to *E. taurica*, Lév., and represent the conidial condition of the species in the earlier and later stages. In the specimens collected of *Oidiopsis sicula* on *Asclepias curassavica* which I have seen, no external mycelium is yet visible, while in those of *Oidium gigasporum* on *Ballota rupestris* mycelial hyphae are evident on the surface of the leaf. Representations of the fungus on *Asclepias* are given in Figs. 5–7 and 29. On *Ballota rupestris* the conidiophores are very laxly branched, and very flaccid, and their origin from the endophytic mycelium is difficult to trace on account of the dense coating of hairs completely covering the under surface of the leaf. I have observed clearly, however, that the fungus sends hyphae into the stomata (see Fig. 18). I have lately received from Prof. F. Bubák examples (unnamed) of the same form collected in Montenegro on *Ballota acuta* (= *B. rupestris*), and in these specimens young perithecia of *E. taurica* are visible on the external mycelium among the conidiophores.

Magnus has recently published (8) a fungus, growing on *Asteriscus aquaticus* (= *Odontospermum aquaticum*) at Santa Cruz, Teneriffe, as a new species under the name of *Erysiphe Asterisci*[1]. I have seen the examples sent out in Rabenh.-Pazschke, Fungi europ. et extraeurop., ed. nov., ser. 2, nr. 4350, and after a careful examination have failed to find any distinguishing characters from *E. taurica*. The perithecia, which are semi-immersed in the persistent felted mycelium, measure 200–240 μ in diameter, and when dry become strongly concave or 'pezizoid' in the manner characteristic of *E. taurica*; the asci are numerous, and large, and contain two ascospores more or less immature. In all respects, in fact, *E. Asterisci* is typical *E. taurica* as regards the perithecial characters; and it is somewhat curious that Magnus in his diagnosis should have omitted to have compared the fungus with this species (especially as *Odontospermum* had been recorded as

[1] The name (without diagnosis) appears in Engl. Bot. Jahrb. xxxiii, 486 (1903).

a host-plant of *E. taurica*) whilst mentioning '*E. Linkii*, Lév.' and *E. Cichoracearum* DC. Magnus makes the following observations with regard to the conidial stage: 'Die Art ist schon durch ihre Konidien sehr ausgezeichnet. Die Konidien sind ausserordentlich lang gestreckt. Sie sind durchschnittlich 52,5 μ lang und 16,5 μ breit. Ihre Oberfläche ist körnig rauh. Sie werden dicht an der Basis von den Konidienträgern schon abgeschnürt. Wohl in Zusammenhang mit ihrer bedeutenden Länge traf ich sie niemals kettenförmig am Konidienträger, sondern immer nur einzeln an demselben.' It may be mentioned here that already in 1900 (2, p. 221) I had pointed out that the conidia of *E. taurica* were remarkable for their large size, frequently measuring 50 × 18 μ. The conidia which occur in the examples of *E. Asterisci* in Rabenh.-Pazsch., nr. 4350, in the Kew Herbarium, measure 40–65 × 15–20 μ, and show the characteristic shape for *E. taurica* (see Fig. 37). I have no hesitation in sinking *E. Asterisci* to a synonym of *E. taurica*.

I have ascertained the presence of endophytic mycelium, sending out hyphae and branched conidiophores through the stomata, in dried examples of *E. taurica* in the perithecial stage on the following host-plants: *Clematis songarica*, *Peganum Harmala*, *Centaurea dissecta* subsp. *Parlatoris*, *Verbascum Blattaria*, *V. phlomoides*, *V. Lychnitis*, *V. bithynicum*, *V. Thapsus*, *Althaea kurdica*, *Euphorbia lanata*, *Carlina lanata*, *Helianthemum oelandicum*, *Psoralea drupacea*, *P. bituminosa*, *Acanthophyllum glandulosum*, *Hedysarum Falconeri*, *Artemisia Dracunculus*, *Odontospermum aquaticum*, *Daucus maximus*, *Nepeta podostachys*, *Astragalus sp.*, *Zygophyllum Fabago*, *Vicia tenuifolia*, *Passerina annua*, *Teucrium Chamaedrys*, *Chondrilla juncea*, *Chrozophora tinctoria*, *Capparis spinosa*, *Cousinia concinna*, *Foeniculum vulgare*, *Phlomis Herba-venti*, *Marrubium peregrinum*, *Cynara Cardunculus*, *Scutellaria multicaulis*, *Cleone arabica*, *Ballota rupestris*, *Epilobium hirsutum*. I have seen examples in the conidial stage only on *Onobrychis viciaefolia*, *Asclepias curassavica*, *Cistus monspeliensis*, *Ruta Buxbaumii*, and *Mimulus glutinosus*.

In my 'Preliminary Note' (1) I pointed out that *E. taurica*, on account of its possession of certain anomalous features described above, viz. the endoparasitic mode of life and the morphological peculiarities of the conidiophores, would probably require to be separated as a distinct genus. In a paper appearing soon afterwards (6), Maire reported that he had discovered an endophytic mycelium in an example of *E. Cichoracearum* DC. on *Cirsium eriophorum*. The example in question, which is contained in Montagne's herbarium in the Paris Museum, was referred to *E. taurica* by Léveillé. The fungus clearly belongs, however, to *E. Cichoracearum*, as here pointed out by Maire, and previously by me in 1900 in my monograph. I have been able to re-examine this fungus, and have seen the original examples from Montagne's herbarium, and also a fragment of the same

specimen used by Maire in his examination. I was able to ascertain that in these specimens the conidiophores arise from superficial hyphae of the mycelium, and that these hyphae send haustoria into the epidermal cells. I was not able to observe any endophytic mycelium in the specimens I examined. In face of the presence of the normal *Oidium*-type of conidiophore borne by ectoparasitic hyphae, I see no reason to doubt that this fungus on *Cirsium* is *E. Cichoracearum*, and I suspect that the endophytic hyphae (which Prof. Maire tells me in a letter he observed in two or three instances) belonged to some other parasitic fungus.

I am still of the opinion that *E. taurica* is distinct generically from the other members of the Erysiphaceae in its completely endophytic habit during the early part of its conidial stage, and in the production of usually branched conidiophores sent up through the stomata. I propose to establish for the reception of this genus, which must bear the name *Oidiopsis*, a new Sub-family, *Oidiopsideae*, with the following characters :— Mycelium at first wholly endophytic, producing conidiophores sent up through the stomata; perithecia produced on the hyphae of a superficial mycelium originating from the endophytic mycelium.

The generic characters of *Oidiopsis* as defined by Scalia will require to be considerably extended. Scalia described his genus from the single example of the fungus in the conidial condition on *Asclepias curassavica*, at a stage when no superficial mycelium occurred. We have then to add to the characters given the presence of the hemi-endophytic mycelium on the surface of the leaf (during the later stage of the conidial condition, and throughout the perithecial stage), originating from hyphae sent up through the stomata, and the generic perithecial characters proper to the fungus in its perithecial stage, viz., those of the fungus hitherto known as *Erysiphe taurica* Lév. The genus, then, will stand as *Oidiopsis* Scalia (emend.), and the species as *O. taurica* (Lév.).

The Family Erysiphaceae will consist of three Sub-families: 1. **Erysipheae**, in which the mycelium is wholly external to the tissues of the host-plant, the hyphae sending haustoria into the epidermal cells alone, or, in one species (*Uncinula Salicis* (DC.) Wint.), into the sub-epidermal cells as well[1]. Genera: *Podosphaera*, *Sphaerotheca*, *Uncinula*, *Microsphaera*, *Erysiphe*. 2. **Phyllactinieae**, in which the conidiophore and perithecium are borne on superficial mycelium, which does not form haustoria in the epidermal cells, but sends down through the stomata special branches, of limited growth, which send haustoria into cells of the mesophyll-tissue. 1 genus, *Phyllactinia*. 3. **Oidiopsideae**, with the characters given above. 1 genus, *Oidiopsis*.

Thus within the Family Erysiphaceae we pass from ectoparasitism, through a hemi-endophytic form, to endoparasitism.

[1] See Grant Smith (13).

The discovery of the existence of an endophytic member of the Erysiphaceae leads us naturally to ask the question whether the fact will have any bearing on the subject of the phylogeny of the group. If we find reason to believe that the endophytism is a primitive character, then we may seek relationship for the conidial stage of *O. taurica* with the genera *Ovularia* and *Ramularia*. In species of these two genera, the conidiophores emerge through the stomata in bundles from an endophytic mycelium just as in *Oidiopsis*; we find, too, in certain species of *Ovularia* and *Ramularia* a vague branching of the conidiophore and laterally borne conidia (cf. Fig. 2). On certain of its host-plants (e.g. on *Asclepias*) *O. taurica* causes, as a result of its parasitism, discoloured spots on the surface of the leaf which are limited by the midrib and its branches; the same habit, it may be noted, is found in species of *Ovularia* and *Ramularia*. On the other hand, we may find reason to believe that the endophytism of *O. taurica* is not a primitive character, but one acquired by the species to meet certain special conditions, and that it bears no phylogenetic significance. Valuable evidence bearing on the point will probably be obtained when the entire process of the germination of the conidium and ascospore of *O. taurica*, and the first establishment of the endophytic mycelium, have been thoroughly investigated.

Some remarks may here be made on the distribution and habitats of *O. taurica*. From the recorded distribution the species is seen to be a lover of warm or dry localities, being found most commonly in the hot dry countries of Central Asia, such as Turkestan, Persia, India, Syria, and Turkey. The species occurs also frequently in South Russia and the Crimea, Bulgaria, Greece, Italy, and Sicily, and has been likewise found in France, Spain, Germany, Hungary, and Algeria. The occurrence of the species in America (California) is noted below. The distribution of the plant shows on the whole that the species is peculiarly fitted to exist under xerophytic conditions. In Turkestan (Seravschan), at a height of 6,000 feet, *O. taurica* is found abundantly—occurring up to 4–5,000 feet on almost all the plants of the steppes. The species is reported as being abundant, also, about the central part of Karakoum, Central Asia. In India it has been collected between Lama Yara and the Phatu Pass, where it must be exposed to very dry winds. Indian specimens, collected by Mr. J. F. Duthie, were found growing on *Hedysarum Falconeri* under practically desert conditions. Examples (now in the Kew Herbarium) growing on *Zygophyllum Fabago* were collected by Dr. O. Stapf at Ispahan, in Persia, where a xerophytic desert or desert-steppe type of flora exists. The species occurs also commonly on plants growing in the deserts of Syria, Kurdistan, Palestine, &c.

It seems very possible that *O. taurica*, by acquiring or retaining the endophytic mode of life, has been enabled to grow in dry, hot countries, the

endophytism serving to meet the need of the fungus to shelter its mycelium in the early stages of the conidial condition from dry burning winds or hot sun, or being due to the inability of the fungus to pierce the thick cuticle of xerophytic plants for the formation of haustoria, and the consequent need to enter the plant in order to obtain nourishment[1]. It must be noted, however, that in a few cases *O. taurica* is found on leaves possessing a cuticle which other members of the Erysiphaceae are able to pierce, thus both *O. taurica* and *E. Cichoracearum* are found on *Verbascum Lychnitis* and *V. phlomoides*.

The fact of the occurrence of an endophytic member of the Erysiphaceae must be remembered in future when discussing the significance of the case of induced endophytism under cultural conditions of a normally ectoparasitic species (*Erysiphe Graminis* DC.) which I have lately reported (4).

A very interesting fact is the possession by *Oidiopsis* and *Phyllactinia* of certain well-marked characters common to both. We find in these two genera the following characters marking them off from the other genera of the Erysiphaceae:—a hemi-endophytic superficial mycelium; lateral appressoria-like organs on the superficial mycelial hyphae; conidia distinguished by their large size[2], the nature of the epispore, and variability in size and shape; and finally, as is noted below (p. 197), the production on certain hosts of a well-marked variety showing constant and distinctive morphological characters which are very similar in both species.

These points of resemblance would seem to show either that *Oidiopsis* and *Phyllactinia* are related phylogenetically, or that they have each been modified in the same direction under more or less similar conditions.

We will now consider the variation in shape and size which is shown by the conidia. As can be seen by reference to Plate XIV, the conidium is sometimes cylindrical with rounded ends, 50–80 × 12–20 μ; more often it is ovoid, oblong, or subcylindric, often distinctly narrowed and more or less sub-acuminate towards the apex, 35–82 × 13–23 μ; or it may be broadly oblong, and rounded at both ends, 38–60 × 20–28 μ. Very rarely the conidium is quite small, oblong and rounded, truncate at both ends, and measuring only 22–32 × 13–16 μ. It is very probable that the great differences in shape and size shown by the conidium, even on the same host-plant, may to a certain extent be correlated with the position of the conidium on the conidiophore. The first conidium produced on the main axis differs probably from those subsequently produced, and both of these

[1] Maire (6) remarks: 'Le mycelium endophytique n'est qu'une adaptation à un hôte xérophyte et à un climat sec.'

[2] The large size of the conidium is perhaps due to the need of the germ-tube to be provided with sufficient food-material to enable it to grow on the surface of the leaf until it finds a suitable stoma to enter. Very probably the germ-tube requires to form one or several appressoria before it enters the stoma.

again may differ in size if not in shape from the conidia produced on the branches of the first and second order [1].

Maire describes (6) the conidium as follows: 'conidiis cylindraceis vel oblongo-cylindraceis, vel ovoideo-oblongis, utrinque retusis, vel apice attenuatis, 50–70 × 15–18 μ'. Two varieties are then founded by this author with the following characters: 'var. *Duriaei* (Lév.) A typo differt conidiis minoribus, 38–45 × 14–18 μ', on *Phlomis Herba-venti* and *P. pungens*; and 'var. *Zygophylli* R. Maire. A typo differt conidiis longe cylindraceis, 57–72 × 13–14 μ', on *Zygophyllum Fabago.*

An examination of a large number of examples of the conidial stage of *O. taurica*, on thirty-seven species of its host-plants, has convinced me that we cannot separate satisfactorily varieties on the characters here given.

The character, viz. the size of the conidium, 38–45 × 14–18 μ, given as distinctive of the 'var. *Duriaei*', does not hold good. In an authentic specimen of '*E. Duriaei* Lév.', from Léveillé's herbarium, at Kew, the conidia measure 43–60 × 18–23 μ (Fig. 24). This example occurs on *Phlomis Herba-venti.* In the example on *P. pungens* sent to me by Prof. Maire as '*E. taurica* var. *Duriaei*' the largest conidia measure 50 × 20 μ; mixed with these are remarkably small ones—the smallest I have seen—measuring only 22–32 × 13–16 μ (Fig. 22). Conidia as small as 28 × 13 μ occur mixed with conidia measuring 60 × 25 μ on *Verbascum Thapsus* (Fig. 23) and *V. Lychnitis*; on *Euphorbia lanata* (Fig. 38) the conidia range from 35–55 × 14–25 μ, and on *Cynara Cardunculus* from 35–50 × 15–20 μ. Similar cases are quite common.

The characters put forward as distinctive of the 'var. *Zygophylli*' are even less satisfactory. In the example sent to me by Prof. Maire the conidia measure 60–73 × 13–20 μ; their shape is shown in Fig. 22**. In an example on the same host-plant, collected by Dr. O. Stapf in Persia, the conidia vary from 45–60 × 14–18 μ, and often depart from the cylindrical shape (Fig. 27). Cylindrical conidia measuring 85 × 16 μ occur intermixed with oblong-elliptic conidia measuring 44 × 22 μ, on *Ruta Buxbaumii* (Fig. 28). Exactly similar cases are found in the forms of the fungus on *Asclepias curassavica* (Fig. 29), *Nepeta podostachys* (Fig. 34), *Capparis herbacea*, *Psoralea bituminosa*, and *Passerina annua* (Fig. 36).

On certain host-plants, however, we do find a well-marked, constant, and distinctive variation in the shape of the conidium. I first met with this in an example, in the conidial stage only, sent to me by Prof. L. M. Underwood, from the Herbarium of the Columbia University, labelled

[1] Scalia says of *Oidium gigasporum*, 'Conidiis catenulatis cylindraceis vel fere ovalibus, apicali sursum acutato, caeteris utrinque truncatulis,' and 'the terminal conidium is usually attenuated at the apex, and truncate at the base, while the others are cylindrical and rounded at both ends and roughly oval.' The same author writes of *Oidiopsis sicula*, 'conidiis catenulatis, conidio apicali sursum longe papillato, basi truncato, rotundato, caeteris cylindraceis, utrinque rotundato-truncatulis.'

'*Oidium obductum*, Ell. & Lang. *f. Mimuli*, E. & E., on *Mimulus glutinosus*. Berkeley, California. (W. C. Blasdale.)' On examination, this was found to be the conidial stage of a fungus possessing endophytic mycelium and branched conidiophores emerging through the stomata of the leaf (Figs. 11–13). In these characters it resembled *O. taurica* in its conidial stage, but the conidia of this fungus on *Mimulus* differed at first sight in being thick, uniformly oblong or cylindrical, and usually more or less angular in outline. This difference in the shape of the conidium, together with the fact that *O. taurica* has not hitherto been reported from America [1], inclined me at first to the belief that the fungus might prove to be a new species of *Oidiopsis*, endemic to America, and distinct from the Old World species. On examining, however, further material of *O. taurica* on its numerous hosts in Europe and Africa, I discovered conidia of the same type in three cases, viz. on *Daucus maximus* from Greece, on *Chondrilla juncea* from Hungary, and on *Foeniculum vulgare* from Algeria. As in these cases perithecia are present, it seems clear that the American plant belongs to *O. taurica*. The plant on *Daucus maximus* was published as a new species under the name of *Erysiphe lanuginosa* by Fuckel in 1871, the specific characters relied upon being certain mycelial and perithecial ones which proved, however, not to be distinctive (see 2, p. 218). In the diagnosis given, the conidial stage is thus described: 'Fungo conidiophoro dense lanuginoso-tomentoso, candido, late effuso, caules foliaque tota occupante, conidiis oblongo-ovatis, utrinque obtusis, hyalinis, 32 mik. long., 16 mik. crass.'

I consider the distinctive shape shown constantly by the conidium in all the examples examined on these four host-plants (*Mimulus glutinosus*, *Daucus maximus*, *Chondrilla juncea*, and *Foeniculum vulgare*) of sufficient value for the separation of the plant as a variety, and I propose to use the name of *lanuginosa* (Fckl.) in giving the present form varietal rank.

The occurrence of *O. taurica*, in the conidial stage only, in a single locality in North America is a very surprising fact; it seems, too, somewhat unlikely—considering the careful attention that has been paid to the Family by numerous mycologists in the United States—that the perithecial stage occurs frequently, if at all.

I should like here to draw attention to the curious case of parallel variation shown by *O. taurica* and *Phyllactinia corylea*. As I have lately pointed out (5), we find a marked variety of *P. corylea*, distinguished by the shape of the conidium, on certain of its host-plants. Now the shape of the

[1] It may be pointed out here that the fungus occurring on *Euphorbia* sp., in the Argentine Republic, lately published by Spegazzini (14) as *E. taurica* Lév., var. *andina*, does not belong to *E. taurica*. As recorded in my Supplementary Notes (3, p. 191), this fungus on *Euphorbia*, while much recalling *E. taurica* in habit, and in the large size of some of the perithecia and their asci, clearly belongs to *E. Cichoracearum* DC. I have lately re-examined the authentic example in the Kew Herbarium, and can state that it shows the ectoparasitic mycelium and the conidial (*Oidium*) stage characteristic of *E. Cichoraccarum*.

conidium in this variety, which I have called *angulata*, is very closely similar to that found in the variety *lanuginosa* of *O. taurica*, as may be seen by comparing Figs. 11–15, 30–33 in Pl. XIII, XIV with those given in my recent paper on *Phyllactinia* (5, Pl. XIV). Moreover, there is a similarity shown by the two varieties in their distribution and promiscuous choice of hosts,—*P. corylea*, var. *angulata*, being found in the United States on *Quercus*, *Castanea*, *Fagus*, and *Ulmus*; in South America on *Adesmia*, and in Europe on *Hippophaë*; and *O. taurica*, var. *lanuginosa*, being found in the United States on *Mimulus*, in Europe on *Daucus* and *Chondrilla*, and in Africa on *Foeniculum*. Further, as pointed out above (p. 195), the two genera have several other common characters.

The conidium of *O. taurica* may be quite smooth or (especially when old) rough with protuberances due to the breaking-up of the epispore; in some cases—as, e. g., in specimens on *Phlomis pungens*, *Odontospermum aquaticum*, *Vicia angustifolia*, *Clematis songarica*, *Cistus monspeliensis*, *Astragalus* sp.—the epispore breaks up almost completely into flakes.

O. taurica is sometimes attacked in its conidial stage by the parasitic fungus *Ampelomyces quisqualis*—a fact which Prof. G. Scalia has independently observed. This parasite, whose life-history was first worked out by De Bary (12), causes a transformation of the conidium, or cell of the conidiophore, attacked, which turns a dark brown (see Fig. 8).

The synonymy of the present species, and its distribution and host-plants—additional to that given in my Monograph (2) and 'Supplementary Notes' (3)—are as follows:—

Oidiopsis taurica (Lév.).

Oidium Haplophylli P. Magn., in Verh. k. k. zool.-bot. Gesell. Wien, l., 445 (1900).

O. gigasporum Scalia, in Rendiconti del Congresso bot. Palermo, 9 (1902).

Oidiopsis sicula Scalia, in Rendiconti del Congresso bot. Palermo, 10 (1902); Scalia, in L'Agric. Calabro-Siculo, xxvii, 396 (1902).

Erysiphe Asterisci P. Magn., in Hedwigia, xliv, 16, Taf. II (1904).

E. taurica Lév., var. *Duriaei* (Lév.), R. Maire, in Bull. Soc. Sci. Nancy, sér. 3, tom. vi, 6 (1905).

E. taurica Lév., var. *Zygophylli*, R. Maire, l. c., pl. ii (1905).

Distrib.—Add Europe: Sicily, Corsica, Montenegro; Africa: Canary Islands, Teneriffe, Santa Cruz.

Hosts.—Add: Asclepias curassavica (conidial stage only), *Ballota rupestris*, *Centaurea dissecta* subsp. *Parlatoris*, *Cistus monspeliensis* (conidial stage only), *Cousinia concinna*, *Chrozophora tinctoria*, *Epilobium hirsutum*, *Onobrychis viciaefolia* (conidial stage only), *Psoralea bituminosa*, *Ruta Buxbaumii* (conidial stage only), *Verbascum bithynicum*, *V. Thapsus*.

var. **lanuginosa** (Fckl.)

Erysiphe lanuginosa Fckl., in Bot. Zeit., 27 (1871).

E. lichenoides, Trab. and Sacc., in Sacc., Syll. Fung., xi, 253 (1895).

A typo differt conidio crasso oblongo vel cylindrico plerumque ambitu plus minusve angulari, interdum medio constricto, 35–70 × 14–28 μ.

Distrib.—**Europe**: Greece, Kephyssos, in Attica (de Heldreich, 1869 and 1871); Hungary, Ménes (Simonkai). **Africa**: Algeria, Ben Chicao, near Medea (Trabut). **N. America**: U. S. A., Berkeley, California (W. C. Blasdale).

Hosts.—Chondrilla juncea, Daucus maximus, Foeniculum vulgare, Mimulus glutinosus (conidial stage only).

Exsicc.—Rabenh. Fung. europ. nr. 1520 (as *E. lanuginosa*); C. Roumeg. Fung. select. exsicc. nr. 6017 (as *E. lichenoides*).

In conclusion, I wish to offer my sincere thanks to the following botanists who have kindly placed valuable material at my service: Professor C. E. Bessey, Professor F. Bubák, M. P. Hariot, Professor P. Magnus, Professor R. Maire, Professor G. Scalia, Dr. H. Sydow, and Professor L. M. Underwood.

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EXPLANATION OF PLATES XIII AND XIV.

Illustrating Mr. Salmon's paper on *Oidiopsis taurica.*

Fig. 1. Part of a branched conidiophore, from an example on *Verbascum phlomoides.*

Fig. 2. Conidiophores and conidia of *Ovularia obliqua* (Cooke), Oud., on *Rumex obtusifolius.*

Fig. 3. Portions of the endophytic intercellular mycelium, growing in the mesophyll of a leaf of *Clematis songarica.*

Fig. 4. Appressorial organs on hyphae of the superficial mycelium; to right, from an example on *Helianthemum oelandicum*; to left, from an example on *Verbascum phlomoides.*

Figs. 5, 6, 7. Young conidiophores emerging through a stoma; the subsequent production of a lateral branch is shown at *x*. From an example on *Asclepias curassavica.* (= *Oidiopsis sicula*, Scalia.)

Fig. 8. Apical portion of two branched conidiophores, both attacked by *Ampelomyces quisqualis.* In one case the apical young conidium has been transformed; in the other, the penultimate cell. Lateral branches have begun to be produced from the conidiophore. From an example on *Verbascum phlomoides.*

Fig. 9. Apical portion of a conidiophore, showing the production of a lateral branch. From an example on *Ballota rupestris* (= *Oidium gigasporum*, Scalia).

Fig. 10. Conidia germinating on a leaf of *Eryngium campestre* (see p. 189).

Figs. 11, 12. Apical portion of a conidiophore and basal portion of another, from an example of the var. *lanuginosa* on *Mimulus glutinosus.*

Fig. 13. A simple conidiophore from the same example, showing the beginning of a lateral branch near the base.

Figs. 14, 15. Apical portions of two branched conidiophores from the same example.

Fig. 16. A branched conidiophore from an example on *Verbascum.*

Fig. 17. Hyphae emerging through a stoma (of the stem); one, to right, forming a conidiophore; one, to left, bearing a young perithecium. From an example on *Passerina annua.*

Fig. 18. Hypha of the superficial mycelium sending a branch through a stoma into the interior of the leaf. From an example on *Ballota rupestris* (= *Oidium gigasporum*, Scalia).

Fig. 19. Apical part of a much-branched conidiophore. From an example on *Ruta* (*Haplophyllum*) *Buxbaumii* (= *Oidium Haplophylli*, P. Magn.).

Fig. 20. Appressorial organs on hyphae of the superficial mycelium, from an example on *Zygophyllum Fabago.*

Fig. 21. Ditto; from an example on *Ballota rupestris* (= *Oidium gigasporum*, Scalia).

Fig. 22. Conidia of *O. taurica* on *Phlomis pungens.*

Fig. 22*. ,, ,, *Cistus monspeliensis.*

Fig. 22**. ,, ,, *Zygophyllum Fabago.*

Fig. 23. ,, ,, *Verbascum Thapsus.*

Fig. 24. ,, ,, *Phlomis Herba-venti.*

Fig. 25. ,, ,, *Verbascum Blattaria.*

Fig. 26. ,, ,, *Peganum Harmala.*

Fig. 27. ,, ,, *Zygophyllum Fabago.*

Fig. 28. ,, ,, *Ruta Buxbaumii.*

Fig. 29. ,, ,, *Asclepias curassavica.*

Fig. 30. ,, *O. taurica*, var. *lanuginosa*, on *Mimulus glutinosus.*

Fig. 31. ,, ,, ,, *Chondrilla juncea.*

Fig. 32. ,, ,, ,, *Daucus maximus.*

Fig. 33. ,, ,, ,, *Foeniculum vulgare.*

Fig. 34. ,, *O. taurica* on *Nepeta podostachys.*

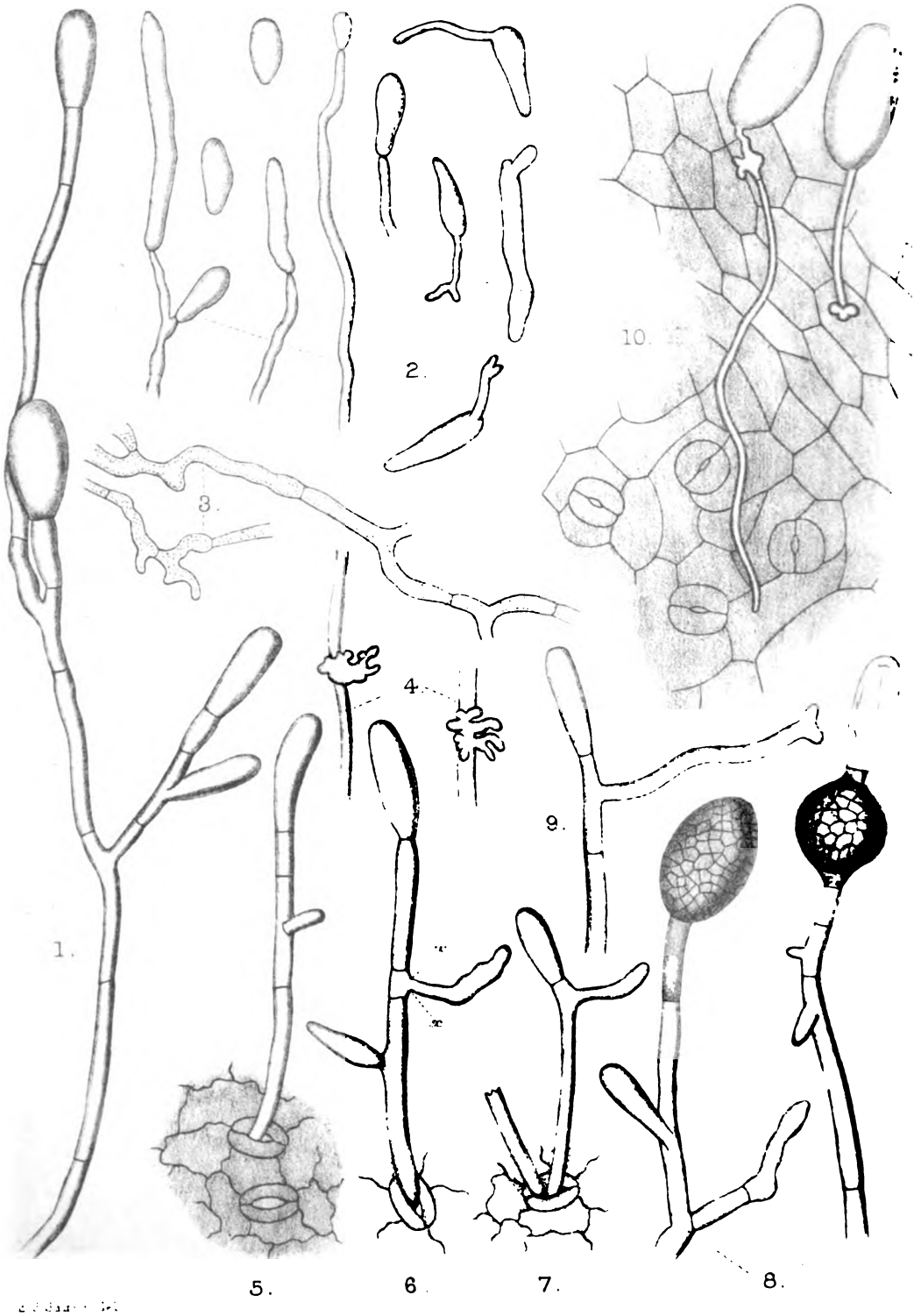
Fig. 35. ,, ,, *Psoralea drupacea.*

Fig. 36. ,, ,, *Passerina annua.*

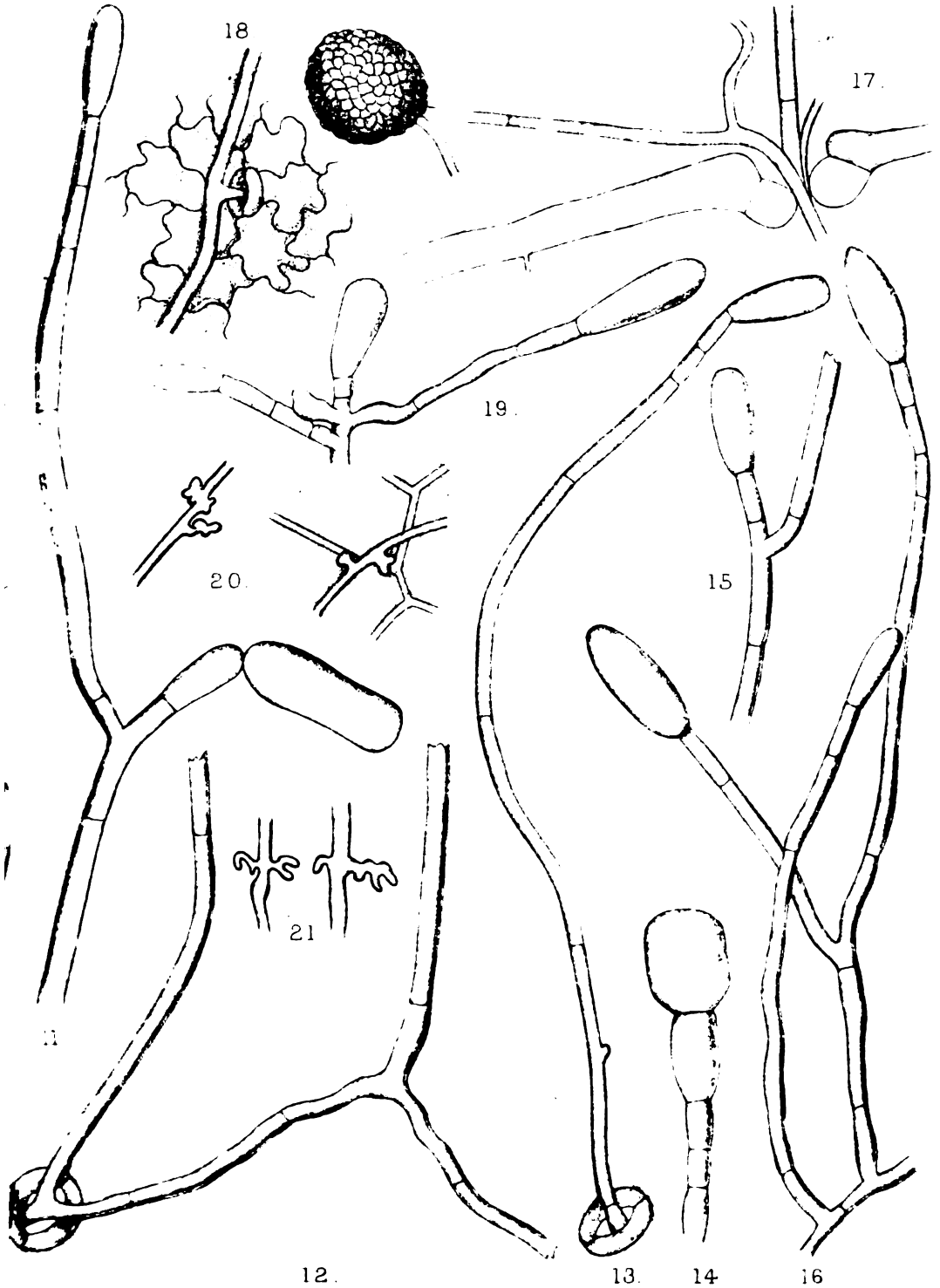
Fig. 37. ,, ,, *Odontospermum aquaticum.*

Fig. 38. ,, ,, *Euphorbia lanata.*

Fig. 39. ,, ,, *Ballota rupestris.*



SALMON — OIDIOPSIS TAURICA.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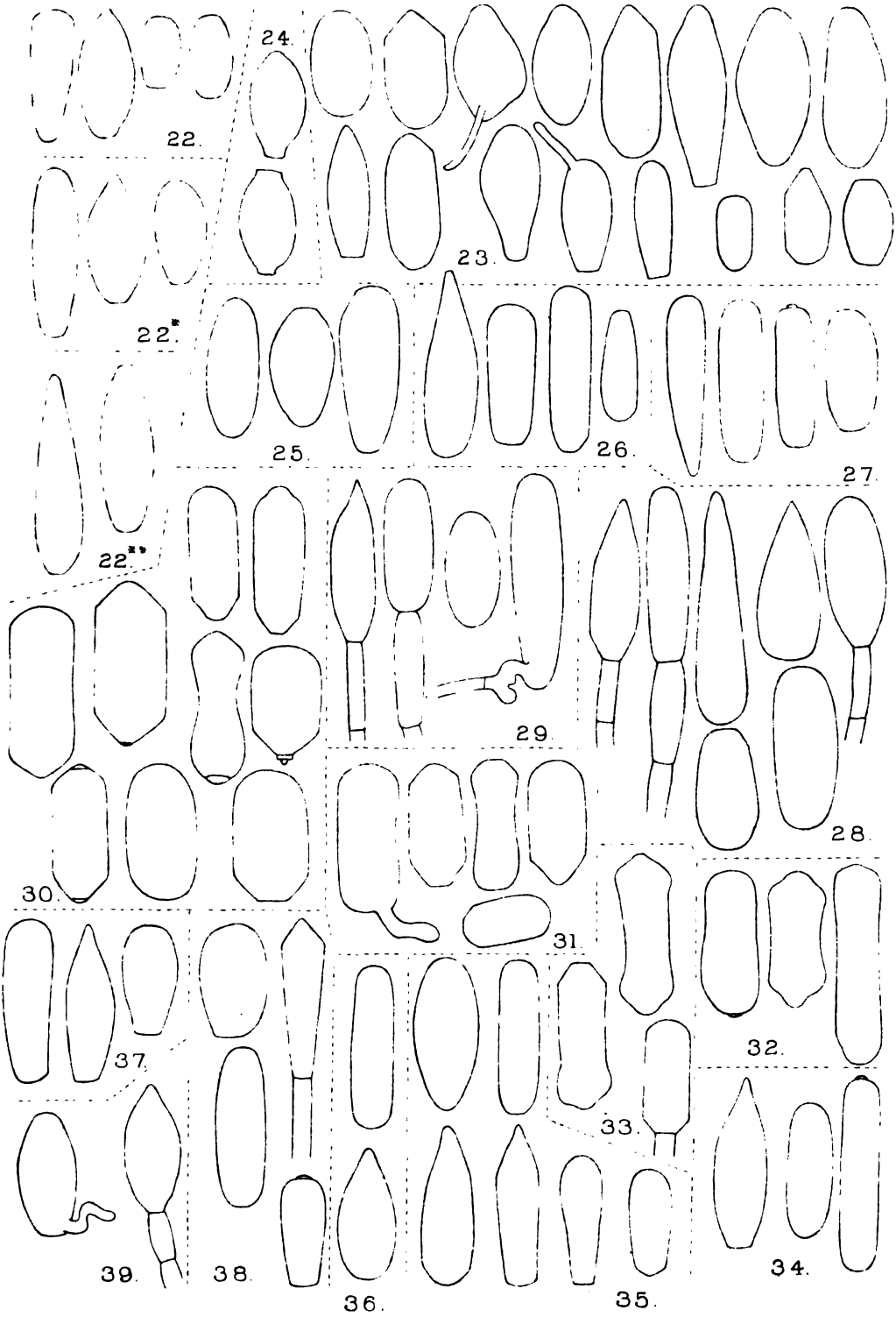

E.S. Salmon del. Huth. arch et imp.

SALMON — OIDIOPSIS TAURICA.

The Formation of Red Wood in Conifers.

BY

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AND

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With Plate XV.

THE formation of red wood on the under sides of the branches of Conifers, which was studied in detail by Hartig, has been variously explained as being due to gravitational stimuli, to variations of pressure and tension, and to differences of illumination on the upper and under sides[1].

The latter explanation has in part been adopted by Sonntag[2], who has recently investigated and compared the mechanical properties of the red and white wood of Conifers.

It is not easy to see what direct effect differences of illumination on the two sides can exert upon the cambium of old stems covered with thick opaque layers of bark.

The only possible action in such cases would be due to the fact that the exposed upper side might be slightly warmer during the day time than the shaded under side.

In the case of *Pinus*, owing to the height of the branches above the ground, the effect of nightly radiation on the relative temperature of the upper and under sides is negligible; and in that of *Cupressus*, since mainly lower branches of compact trees are used, the under side would be more exposed and subject to greater radiation and cooling during the night. Hence, the only possible effective differences of temperature are those produced during the day time.

Sonntag lays main stress upon the influence of pressure, which he considers to be primarily responsible for the production of red wood, the

[1] Cf. Pfeffer's Physiology, Eng. Trans., Vol. ii, p. 108; Vol. iii, p. 416.

[2] Sonntag, Jahrb. f. wiss. Bot. Bd. xxxix, p. 71.

[Annals of Botany, Vol. XX. No. LXXVIII. April, 1906.]

latter appearing, according to him, on the side of an erect tree subjected to compression by the action of the wind.

Even here, however, although the tree may still remain upright, every time it is bent to one side by the wind it is subjected to geotropic action, and a geotropic stimulus, if frequently and rapidly repeated, will produce a geotropic curvature in a root, however short the individual periods of exposure may be.

To investigate these points more fully, a series of experiments were begun upon the main axes and lateral branches of plants of *Cupressus nutkaensis, C. Lawsoniana, Pinus contorta,* and *P. Cembra,* in May, 1905.

The stems were forcibly bent into circular or elliptical forms and fastened in such a fashion that the geotropic and pressure effects were not equally distributed, the former influencing the horizontal portions, whereas the compression was restricted to the inner surface of the ring.

The stems were sawn off and examined in November and December, and the distribution of the red wood is shown by the dark line on the appended figures.

The specimens represented by Figs. 3 and 4 were shaded from above, whereas the others were exposed to normal illumination; and it will at once be seen, by comparing the figures, that they give absolutely no evidence of the existence of the 'heliotropic' action which Sonntag postulates.

It is also evident that it is almost solely the action of gravity, and not that of pressure, which has in these specimens determined the formation of the red wood, for this appears mainly on the under sides, whether they are subjected to compression or tension.

The change from one side to the other is especially well shown in Fig. 1, but can be traced in the others also, the side of the erect portion on which the thin connecting layer of red wood develops being probably determined by the loop being slightly inclined to one side.

It will be noticed that in all cases there is a tendency for the formation of red wood to spread into the vertical regions, where it fades away.

This is, however, the result of the gravitational stimulus spreading from the upper and under surface, where it is directly perceived, to the neighbouring vertical portions, and in this way preventing the weakening effect of an abrupt transition from one type of wood to the other.

The formation of red wood begins first on the under surfaces and then spreads laterally, so that in the outermost vertical or nearly vertical regions to which it extends only a thin superficial layer of the year's annual ring consists of the red tracheides, the inner part being white wood.

Thus, on the under side of the uppermost point of the curvature of a branch the red tracheides averaged thirty-two deep, towards the side of

the curved region the number fell to fifteen, and in the upper part of the vertical region to less than eight.

Hence this last region only received the gravitational stimulus from the horizontal region when three-fourths of the year's growth of wood had taken place.

A few peculiarities will be noted in the figures. Thus in the basal part of Fig. 3 the red wood appears on the upper inner surface of the main axis, on the side of the lower part, and on the inside of the upper part of the vertical segment. The lower part, however, formed but little wood and was very strongly compressed.

Hence it is possible that very strong pressure applied to a feebly active cambium may overcome the gravitational influences normally responsible for this special morphogenic response.

In Fig. 5 red wood appears on both upper and under surfaces of a few lateral branches, although both the gravitational and the pressure stimuli act alike on the under surface. Possibly this is the result of the diffuse spreading of the gravitational stimulus from above and below the branch; and in any case it is worthy of note that a slight deviation from the perpendicular is sufficient to produce a perceptible response, while the maximum possible morphogenic stimulus appears to be exercised by a comparatively small angle of deviation, beyond which but little further increase occurs.

In brief, therefore, it may be stated that, as far as these observations go, they show that the formation of red wood is a morphogenic response to a gravitational stimulus which is able to spread longitudinally from the region where it is directly perceived, and which may under special circumstances be modified or suppressed by very strong pressure stimuli.

NOTES ON FIGURES IN PLATE XV.

Illustrating Messrs. Ewart and Mason-Jones's paper on Red Wood in Conifers.

Fig. 1. Main axis of *Cupressus Lawsoniana*. Red wood very thick at under surface of top of curve, change from one side to the other well shown; the dotted line indicates here, as in all other figures, the distribution of the red wood on the back face of the stem.

As shown in the figure, the straight part of the stem grew slightly out of the perpendicular, also with a slight tilt away from the plane of the paper.

Fig. 2. Lateral branch of *Cupressus nutkaensis*. The upper branch and the thin twigs shown were dead.

This was a very good specimen, inasmuch as gravitational stimulation was practically at its maximum.

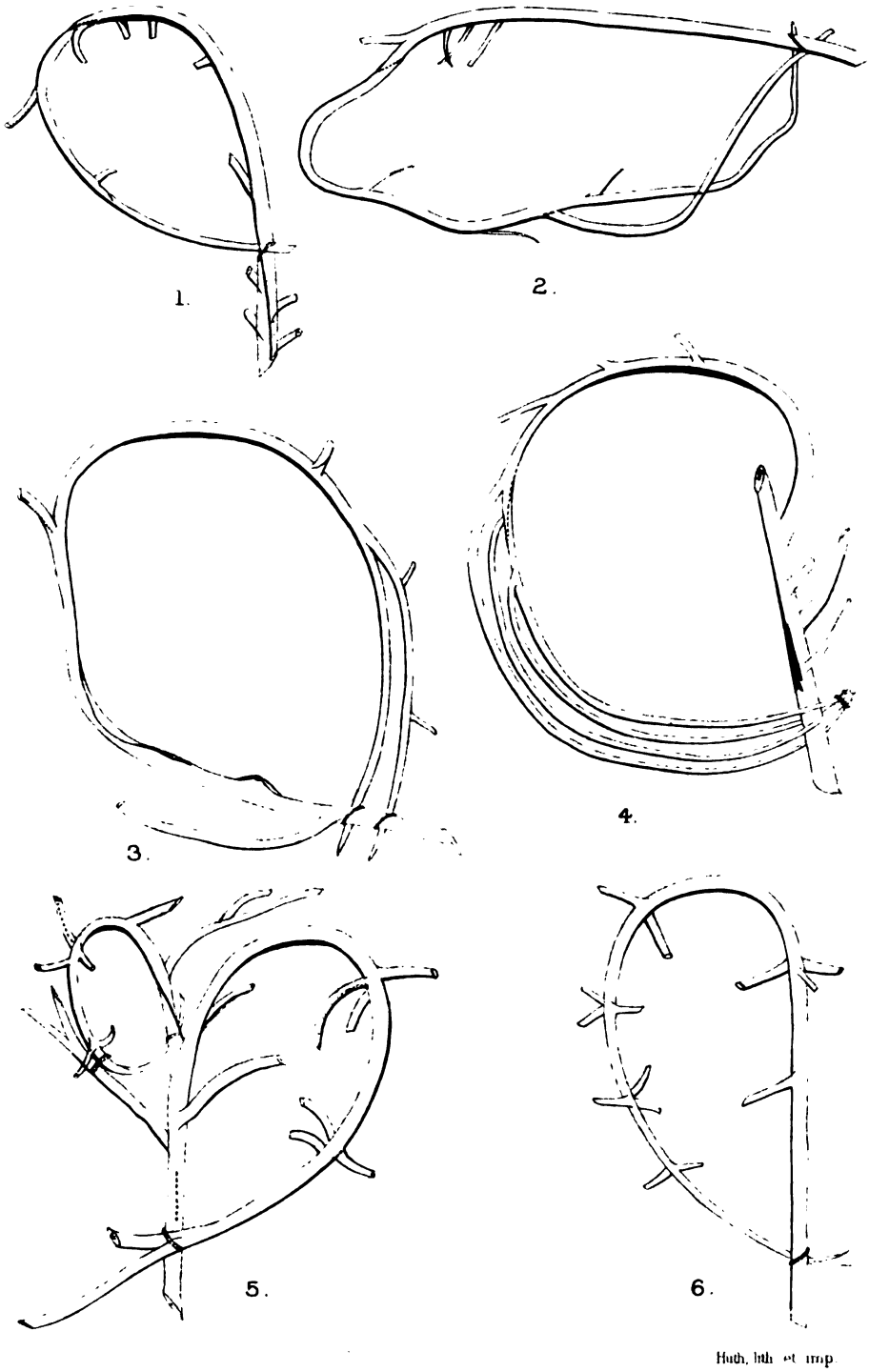
The entire absence of red wood from the region of greatest compression is well shown.

Fig. 3. Lateral branch of *Cupressus nutkaensis* shaded from above; peculiarities in distribution of red wood are mentioned in the text.

Fig. 4. Lateral branch of the same tree as Fig. 3 and under similar conditions of shade.

Fig. 5. Main axis and top branches of *Pinus contorta*. Peculiarities of distribution of red wood are given in the text; the main branches were bent and grew in planes practically at right angles to one another.

Fig. 6. Main stem of *Pinus Cembra*. In this specimen the pigment in the red tracheides is not as strong as in those of the other specimens used, so the stem had to be continually wetted with tap water in order to bring out the colour differentiation of the red and white woods.



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EWART AND MASON-JONES,-RED WOOD IN CONIFERS.

The Statices of the Canaries of the Subsection Nobiles. I.

BY

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IN a communication to the Gardeners' Chronicle of Dec. 17, 1904, Dr. G. Perez, of Orotava, called attention to the now complete disappearance of *Statice arborea* from its last refuge, adding some very interesting remarks on the probability of its having been a hybrid between *Statice fruticans* and *Statice macrophylla*, and the general readiness of the species of the subsection *Nobiles* to hybridize. Since Leopold von Buch [1] declared *Statice arborea* extinct and its subsequent rediscovery, it has, along with its allies, repeatedly been quoted as an instance of the vanishing old flora of the Canaries. Considerable material and much valuable information regarding the Statices of the subsection *Nobiles* having accumulated at Kew during the last few years, almost exclusively through the efforts of Dr. Perez, it appeared to me desirable to bring together what we know of the subject. Certain questions, as for instance those concerning the oecological and biological conditions under which those species still hold their own or slowly vanish, can, of course, not be solved satisfactorily at the distance and from dry material. Still much may be accomplished in the way of preparatory work that cannot be done in the field, and yet is indispensable as a sound starting basis for the more fortunate man who is able to work in Nature's own laboratory.

[1] Allgemeine Übersicht der Flora auf den Canarischen Inseln (1819), pp. 338–9. The Norwegian botanist, Christian Smith, accompanied Buch to the Canaries. His diary was published by F. C. Kiaer in 1889, and in it we find on p. 29 an entry relating that Buch brought him 'Stat(ice) fr(uticosa).' To this Kiaer has added a footnote: '= *Limonium fruticosum*, Mill., *Statice cylindricum*, Forsk. eller maaske = *Statice arborea*, S. 137.' 'S. 137' refers to Buch's Physikalische Beschreibung der Canarischen Inseln (1825), where it says: 'Fuente del Rey, zwischen Puerto Orat. u. Realexo; aber in Gärten. Wo ist sie wild?' Kiaer's synonymy is certainly wrong. What Miller's *Limonium fruticosum* is, I do not know for certain, possibly *Statice axillaris*, Vahl., a species of both coasts of the Red Sea, whilst '*Statice cylindricum*, Forsk.,' or rather '*Statice cylindrifolia*, Forsk.,' as it should read, is a native of Yemen. Chr. Smith very likely meant *Statice arborea*.

[Annals of Botany, Vol. XX. No. LXXVIII. April, 1906.]

All the Statices of the subsection *Nobiles* are endemic in the Canaries, some being restricted to a single locality of very limited extent, others to a single island, and none occur at the same time in more than two of the islands of the archipelago. As they are very conspicuous objects on account of their brilliant blue inflorescences, and to some degree familiar to the inhabitants—they call them 'Siempreviva del mar[1]'—it is not probable that future exploration will add much to their areas as they are known at present. On the contrary, there is a considerable risk of their total disappearance.

The first species of the *Nobiles* group of *Statice* that became known was discovered by Francis Masson, who on his way to South Africa collected in Teneriffe in 1773. He found it, to quote his own note attached to his specimen in the British Museum, 'on a rock in the sea, opposite the fountain which waters port Orotava.' He presented to the younger Linnaeus a specimen which Solander[1] named *Statice arborea*, adding as locality: 'Teneriffa, circa Ramla in rupibus maritimis.' Masson's discovery was, however, not made known until more than forty years later, when, in 1819, J. Smith[1] described it as *Statice arborea* from 'the maritime rocks at Buraao and Rambla in the isle of Teneriffe.' The apparently conflicting statements concerning the locality can easily be reconciled. Buraao is a slip for Burgado, a small cove immediately to the east of the Rambla del Castro, a well-known littoral terrace on the north coast of Teneriffe, about 5 kil. from Puerto d'Orotava. In that cove there are some calcareous springs[2], probably Masson's 'fountain,' and at a stone-throw's distance from the shore two basaltic cliffs on which Berthelot and Webb actually found the plant growing in 1829[3]. Long before that, in 1796, however, Ledru, a botanist who accompanied Capt. Baudin on his expedition to the West Indies, had also collected the plant, but where is not exactly known, nor is there any reference to his find until 1817, when Poiret[4] called attention to it. A few years later, probably very soon after Humboldt's short stay in Teneriffe, it was found again by Aug. Broussonet, an accomplished zoologist and botanist, who at that time was French Consul in the Canaries. Broussonet was soon afterwards appointed Professor in the University at Montpellier, where, in 1805, he published a catalogue[5] of the plants of the Botanic Garden then in his charge, enumerating in it a '*Statice arborescens*, Br.' without any description or other remarks. He distributed, however, at the same time, herbarium specimens of that plant to several botanists, among them also to Willdenow[6], who, in 1809, published a description of it under the name

[1] J. Smith in Rees, Cyclopedia, xxxiv (1819).

[2] Rothpletz in Petermann's Geographische Mitteilungen, xxxv (1889), p. 245.

[3] Berthelot et Webb, Histoire naturelle des Iles Canaries, III, i, p. 8, and iii, p. 181. See also their Atlas, Vues phytostatiques, tab. viii, fig. 3.

[4] Poiret, Encyclopédie méthodique, Suppl. v, p. 236.

[5] Broussonet, Elenchus Plantarum Horti Botanici Monspeliensis anno 1804 (1805), p. 58.

[6] Willdenow, Enumeratio Plantarum Horti Regii Botanici Berolinensis (1809), p. 337.

Statice arborea, the name (not *S. arborescens*) which Broussonet had used on the labels of the specimens of his own herbarium as well as of the duplicates which he gave away. This being the first description of *Statice arborea*, Broussonet also had the credit of the discovery. The locality where he found the plant was not known, or rather it was assumed that it was the same as Masson's. Through the courtesy of Prof. Flahault, I had, however, an opportunity of seeing Broussonet's own specimens, and found that he gives it as 'Sur les rochers au-dessus de la maison à Daute.' Dauté, or El Dauté, is a place about 1 km. to the west of Garachico, and 18 km. to the west of the Burgado Cove. It has not been found again there, and evidently disappeared long ago from that neighbourhood, a district covered with vineyards. When Leopold von Buch stayed in Teneriffe in 1815, he found *Statice arborea* growing in gardens at Fuente del Rey, between Orotava and Realejo, but, as he adds, 'nowhere wild [1].' I have, however, already mentioned that it was in 1829 rediscovered by Berthelot and Webb on the same cliffs in the Burgado Cove where Masson collected it, and it was still growing in that locality in 1858 when Lowe gathered it there. A slight extension of this very small Burgado area became known through Webb, who, in 1845, obtained from Bourgeau specimens of *Statice arborea* from 'rupibus Teneriffae (genitive) oppositis' (that is, opposite to the two Burgado cliffs [2]), or, as Bourgeau himself says on the label (No. 65), from 'La Dehesa de los Frayles.' Here, on the mainland, Dr. Perez places also Gustav Mann's locality, 'La Longera,' where he collected *Statice arborea* in 1863. Since then it has not been recorded again from the cliffs in the Burgado Cove, and Dr. Perez states positively that it has disappeared altogether [3]. I may also add here that it was from the same spot that the plants were derived which Webb sent home—the first in 1829 [4]—and which created such sensation when they flowered for the first time [5].

Up to 1845 or 1846, when Berthelot and Webb issued the part of their Phytographie des Iles Canaries that contained the descriptions of the Canarian Statices, there was no doubt about the homogeneous character of *Statice arborea* as a species, although Webb, in the later part of the *Phytographie* [6], had revived Broussonet's catalogue name *Statice arborescens* in preference to *Statice arborea*, which was up till then in general use, and justly so. In 1846, however, E. Bourgeau, whose name is so intimately connected with the

[1] L. von Buch, Physikalische Beschreibung der Canarischen Inseln (1825), p. 137. See also note 1, p. 205.

[2] Berthelot et Webb, l. c., III, iii, p. 180.

[3] Perez in the Gardeners' Chronicle, 3rd ser., xxxvi (1904), p. 419.

[4] Loudon, Encyclopaedia of Plants, 1855, p. 1330.

[5] This is a passage by Lindley from Botanical Register, 1839, tab. 6, referring to a specimen exhibited by Messrs. Lucombe, Pince & Co.: '6 ft. high, and covered with large clusters of flowers, the brilliancy of whose blue neither precious stones nor metallic preparations could even approach'! For this plant the Gold Banksian Medal was awarded (Proc. Hort. Soc. London, 1838, p. 10).

[6] Berthelot et Webb, l. c., III, iii, p. 180, tab. 194.

botanical exploration of the Canaries as of many other countries, discovered a Statice very similar to *Statice arborea*, but of smaller stature and, above all, with a much reduced stem, and distributed it as *Statice fruticans*, Webb. Of this specimens were sent, probably by Webb, to Van Houtte's establishment in Ghent, where they flowered in 1847, and a description and figure were published by Lemaire[1] in the Flore des Serres early in the following year, the name being changed from *Statice fruticans* into *Statice frutescens*. The plants were not quite 6 dm. high, instead of 12–18 dm. as was the case with *Statice arborea*, and the leaves also were smaller than in that species. Soon after the publication of Lemaire's *Statice fruticans*, vol. xii of De Candolle's *Prodromus* was issued, containing Boissier's monograph of the Plumbagineae. There the author, although aware of Lemaire's publication, adopted Webb's name *Statice fruticans*[2] for the supposed new species, and *Statice arborescens*, Brouss., for the old *Statice arborea*, but with this distinction, that he claimed the specimen which Willdenow had received from Broussonet for *Statice fruticans*, and he consequently quoted *Statice arborea* as synonym under *Statice fruticans*. Some specimen of Broussonet's—it is not specified—was, however, still referred to *Statice arborescens*, that is the arborescent, large-leaved plant, as represented in Webb's own collecting and by the English illustrations[3] of *Statice arborea*. Bourgeau collected the plant, which thus became the 'type' of *Statice frutescens*, Lem. (= *S. fruticans*, Webb ex Boiss.), on a rocky promontory called El Freyle, not far from Cape Teno, the westernmost point of Teneriffe, and it is still there, or at any rate was there until quite recently, when the Rev. R. P. Murray gathered it in 1889. In 1855, however, H. de la Perraudière (Bourgeau's companion on his second journey to the Canaries) collected a Statice at 'P^to^ Orotava, in scopulis maritimis,' which in the Montpellier herbarium lies under the name *Statice arborescens*, Brouss., whilst it was distributed by Bourgeau (No. 1494) as *Statice fruticans*, the locality being quoted by him as 'Dehesa de los Frayles in rupibus maritimis.' I have no doubt that Perraudière's plants came from the cliffs of the Burgado Cove, either those in the sea or those on the mainland opposite. These herbarium specimens of the *Statice fruticans* from Burgado are so similar to those from El Freyle that no botanist would hesitate to sort them together. If we admit Boissier's distinction of *Statice arborescens* and *Statice fruticans*—or, as they should be called, for reasons of priority, *Statice arborea* and *Statice frutescens*—we find that both species grew together in the Burgado area as well

[1] Lemaire in Flore des Serres, 1st ser., iv (1848, March), tab. 325.

[2] Boissier in De Candolle, Prodromus Systematis Naturalis Regni Vegetabilis, xii (1848), p. 636.

[3] Paxton, Magazine of Botany, iv (1838), tab. 217; Maund, The Botanist, i (1838), tab. 47; Botanical Register, xxv (1839), tab. 6; Botanical Magazine (1840), tab. 3776. See also Horticulture Universelle, vi (1845), tab. 164.

as in that of Dauté, whilst *Statice frutescens* alone occurs on El Freyle. But here the question arises, are the two supposed species really distinct, or have we in them simply arborescent and subacaulescent forms or individuals of one species; or, finally, is Dr. Perez right in assuming that *Statice arborea* was a hybrid of *Statice frutescens* with *Statice macrophylla*? Boissier[1] supported his view that they were distinct species by pointing out the differences in stature, in the size of the leaves, the length of the flowering branches, and other less obvious characters, such as the width of the wings of the branches, the shape of the auricles of the spike-bearing branchlets, the presence or absence of cilia on the uppermost (inner) bract, and the width of its keel. I may state at once that these less obvious differences do not hold good. They are slight, and differences of the same degree may be found in one and the same individual plant. On the other hand, it must be admitted that the herbarium specimens can readily be sorted by the dimensions of their leaves and inflorescences into two sets, one corresponding to *Statice arborea* as represented by Webb's and Bourgeau's specimens from the Burgado cliffs, and the other to *Statice frutescens* as represented by Bourgeau's specimens from El Freyle. There are only few cases where one might hesitate. As to stature, the herbarium material, as it is, tells us nothing. Now Broussonet, who is supposed to have collected both species in the same place, mounted both forms on the same sheet in his own herbarium, there being three branches—one with large leaves, and two with small leaves like those of the specimen which he gave to Willdenow—but to him they were no doubt all *Statice 'arborea.'* In a similar way Perraudière himself put the plant collected by him on the Burgado cliffs down as '*Statice arborescens*,' and it was only Bourgeau, the distributor, who, from the similarity of the branches cut by Perraudière and his own from El Freyle, referred them to '*Statice fruticans*,' implying that they had been taken from a subacaulescent plant. It seems clear that neither Broussonet nor those who collected on the Burgado cliffs were ever struck by the presence of two distinct species, such as Boissier suggested. There would, of course, be taller and shorter individuals, and, in the same individual, perhaps robust and weak branches; and it would depend on chance or the idiosyncrasy or object of the collector whether he would cut his specimens from one or the other set of individuals or branches. In fact, there is at present growing in the Temperate House at Kew a fine specimen of *Statice arborea macrophylla*, communicated by Dr. Perez, from which specimens representing either form might be obtained. It, however, also seems to be the case that on El Freyle only a subacaulescent small-leaved form occurs. It has been in cultivation in Europe and in Dr. Perez's garden without chang-

[1] Boissier, l. c., p. 637.

ing its stunted growth ; but this does not seem to prove that that feature has in the El Freyle plant become fixed, as one would expect of a character good enough for specific distinction. If, as I believe, those cultivated specimens were propagated from cuttings, representing short axes of the second or third rank, one would not expect them to behave necessarily like the primary axis of *Statice arborea*, which seems to have a natural tendency to grow, under favourable circumstances, into an erect leafless stem, bearing at its top on short branches a compound rosette of leaves, otherwise very like that which in the other stemless species rests on the ground. But even if it should not be possible to raise the arborescent form from the seed of the stunted Statice of El Freyle, it would hardly stand to reason to treat it as a species on that account only.

Now as to Dr. Perez's theory[1] of hybridization referred to in the introductory lines of this paper. He assumes that the arborescent form, the *Statice arborea* or *Statice arborescens* of the authors, was a hybrid of *Statice 'fruticans'* and *Statice macrophylla*. In support of this he points out that in the Botanic Garden at Orotava there was growing until lately a very old specimen representing in his opinion the now extinct typical (i. e. arborescent) *Statice arborea*, and more or less intermediate between the suggested parents, and that this is also the case with the daughter plants raised from the former ; and secondly that *Statice 'fruticans'* and *Statice macrophylla* actually grew together in the Burgado Cove. *Statice 'fruticans'* and *Statice macrophylla* are plants easy enough to distinguish. Both have a short primary axis with the ramification and leaf-arrangement in compound rosettes, so common in *Statice* ; but the blades of the former are small and contracted into a long petiole, whilst they are large, lanceolate to obovate-oblong, and long-attenuated at the base, and practically sessile in *Statice macrophylla*. The wings of the flowering branches of *Statice 'fruticans'* are narrow, and those of the ultimate branchlets produced into acute, often sickle-shaped auricles ; but they are broad and produced into obtuse auricles in *Statice macrophylla*. Further, *Statice 'fruticans'* has glabrous or almost glabrous inner bracts with a laterally compressed obtuse keel near the apex and a very narrow, scarious margin. In *Statice macrophylla*, however, these bracts are whitish-pubescent, rounded on the back without a keel, and bordered towards the apex with a broad, blue, crisped frill. The flowers are finally somewhat larger in *Statice macrophylla* than in *Statice 'fruticans.'* Dr. Perez has supplied me with photographs and ample dried material of the Orotava garden plant mentioned above.

The first thing that strikes one is that the supposed hybrid shows an arborescent habit which is altogether absent in the parents. As to the leaves, they are very large and rather intermediate between those

[1] Perez in the Gardeners' Chronicle, 3rd ser., xxxvi (1904), p. 419.

of typical *Statice arborea* and *Statice macrophylla.* The wings of the branches are more developed than in *Statice* '*fruticans*,' and the wing-auricles as a rule obtuse as in *Statice macrophylla.* The bracts again have the characteristic pubescence of *Statice macrophylla*, and also frequently a small blue frill, whilst the dorsal keel is much less distinct than in *Statice* '*fruticans*' and overtopped by the frill. The flowers, finally, are certainly larger than in *Statice* '*fruticans.*' Compared, however, with the finest specimens of *Statice arborea* collected by Webb and Bourgeau and the figures[1] of the plants of that species grown in England between 1830 and 1850, the supposed hybrid of the Orotava garden agrees with them much more than with *Statice* '*fruticans*,' the main differences being in the marked pubescence of the inner bract, the reduction of the dorsal keel, and its tendency to run into a frill. As to the auricles of the ultimate branchlets, I would remark that their shape is fairly constant in *Statice macrophylla*, but rather variable in *Statice arborea* (including *Statice* '*fruticans*'). The Orotava garden plant may therefore have been very well a descendant of a specimen of the typical *Statice arborea* growing in the garden by the side of *Statice macrophylla*, and therefore exposed to the chances of fertilization from the latter. I admit readily its hybrid character, but the parents would be typical *Statice arborea* (not *Statice* '*fruticans*') and *Statice macrophylla.* Otherwise we would, indeed, have to assume that the reduction of the stem in *Statice* '*fruticans*' is so little fixed a character that the latent tendency towards the arborescent habit, which it might have inherited from its ancestors, could assert itself in the cross product with *Statice macrophylla* to such a degree as to become quite paramount. However that may be, it seems to me a perfectly untenable hypothesis that the arborescent *Statice* from the Burgado cliffs itself could have been a cross between the stunted *Statice* '*fruticans*' and *Statice macrophylla*, free as it is from any taint traceable to the latter.

As to the presence of *both* supposed parents on the Burgado cliffs we have no clear evidence. I have already pointed out that the assumption of the former occurrence of *Statice* '*fruticans*' in that locality rests chiefly on Bourgeau's determination of some specimens which Perraudière collected there in 1855. Of more importance is the fact that there is at Kew a sheet of *Statice macrophylla* collected by Gustav Mann in 1863 with the indication 'La Longera.' This 'La Longuera,' as it ought to be spelled, Dr. Perez says is a place not more than a stone-throw's distance from the Burgado islets. I have, of course, no reason to doubt that there is some locality of that name in the Burgado Cove, the less so as Mann's specimen of *Statice arborea*, also marked 'La Longera,' points to that

[1] See note 3 on p. 208.

neighbourhood. But, as *Statice macrophylla* has never been observed by any one else in this locality, but only some distance to the east of Orotava, I would suggest the following explanation. On both labels Herr Mann adds after 'La Longera' in brackets: 'sea coast.' May he not have meant in both cases 'La Longuera' simply to stand for sea coast or shore, not considering it necessary to be more precise? 'Longuera' in Spanish means any long and narrow strip of land, and so he may have used it as 'nomen genericum,' whilst to a native of Teneriffe 'La Longuera' would be the Longuera κατ' ἐξοχήν and some perfectly definite spot, such as the shore opposite the Burgado rocks.

Considering all the circumstances, it seems quite certain to me that the typical and now extinct *Statice arborea* of Masson and Broussonet was a perfectly distinct species which inhabited at some time within the last 110 years two very small areas on the north coast of Teneriffe, one at the Burgado Cove, the other at Dauté, whilst a third equally small area, on the El Freyle, harbours still a much stunted form of it. Whether the latter formerly occurred along with the arborescent state in the other two areas we do not know, nor how far its subacaulescent habit has become fixed or is merely the result of the conditions of the habitat. It may, however, for the present, be distinguished from typical *Statice arborea* as *Statice arborea* forma *frutescens*. Plants of *Statice arborea* were early taken into cultivation in Teneriffe, and the specimens now in possession of Dr. Perez, and (one) of Kew are descendants of the extinct species with a distinct strain of *Statice macrophylla*.

NOTE.

NOTE ON THE FOLIAR ORGANS OF MONOPHYLLAEA.—The small genus of Cyrtandraceae, *Monophyllaea*, comprises seven species of soft succulent herbs growing on limestone rocks from Southern Siam southwards to the Malay Peninsula, Sumatra, and Borneo. The species are all very similar in appearance and habit.

Monophyllaea Horsfieldi Br. A native of the Malay Peninsula; has been in cultivation in the Botanic Gardens, Singapore. It is a monocarpic plant, with a cylindric succulent stem, slightly dilated at the base, where it emits numerous rootlets. In a large plant the stem is about 6 inches tall, and half an inch through; on the top are borne two foliar organs, of which one is very much the larger, attaining a length of 12 inches and a width of 18 inches. The leaf is ovate-cordate and sessile, with nerves radiating from the base. It is thinly fleshy, and more or less sprinkled with hairs. The opposite leaf is very small. From the axils of these leaves rise four or five slender peduncled scorpioid cymes of small white flowers.

The seeds are borne in a small capsule, and are minute, elliptic, with a reticulated testa.

On germination two small, equal, semicircular, rounded cotyledons appear, rather broader than long. Very soon, however, as the young plant grows, one becomes more oblong, and longer than broad. It is now larger altogether than the other. After a week or two the larger one, increasing in size more rapidly than the other, becomes ovate-cordate with a blunt tip, and the midrib and lowest pair of nerves are faintly visible. The other leaf, though it increases in size, retains its original form, but is now not a quarter of the size of the big leaf. When the latter is half an inch long, it shows its complete nervation, and becomes slightly hairy along the lower edge. The smaller leaf is now concealed under the lobes of the cordate bigger leaf. As the plant grows, no buds appear on the stem below the leaves, and there are no leaf-buds in the axils of the two leaves.

Thus, in *Monophyllaea*, there is no stem except the original hypocotyl, and no leaves other than the two original cotyledonary leaves, of which one practically becomes abortive.

In 1861 Mr. Crocker (*Journal Linn. Soc.*, vol. II, p. 65) showed that the two very unequal leaves of *Streptocarpus polyanthus* were the permanent cotyledons, and that the plant was leafless except for one or two upper leaves, unless the bracts of the inflorescence were considered as such.

Mr. Clarke (*Monogr. Cyrtandr.*, p. 12) suggests that in other one-leaved species of Cyrtandreae of various genera the one large leaf may also be the cotyledon. He instances *Didymocarpus pygmaea*, *Trachystigma Mannii*, *Acanthonema strigosum*,

Epithema Horsfieldi, and all the six species of *Monophyllaea*, and says that 'if it should appear that the solitary leaves of these are really permanent cotyledons, it will be an additional proof of the very close connexion between different genera of the tribe.' Certainly in *Monophyllaea* the only foliar organs are the cotyledons. In adult plants the smaller cotyledon usually disappears, and I cannot see any bracts, even, in any of the specimens. Of the other plants of this habit mentioned by Mr. Clarke, *Trachystigma*, *Platystemma*, and *Acanthonema* have bracts, and of *Didymocarpus pygmaea* Mr. Clarke says, 'Bracts none, or inconspicuous.' *Epithema* has often fully-developed normal leaves, and a large cup-shaped bract at the base of the flowers. A plant of very similar habit to *Monophyllaea* is *Argostemma unifolium* King. This has a succulent stem swollen tuberously at the base, and a large rounded leaf from the axil of which arise one or more peduncles. This Rubiaceous plant grows on rock faces, as *Monophyllaea* does. I have not had any opportunity of raising it from seed, but it is clear, I think, that in this plant the large leaf is not one of the cotyledons, for half-way up the stem, below the large leaf, is a pair of ovate scale-like leaves showing the presence of a node. These may be remains of cotyledons, but it is obvious that the upper leaf is not. Further, the large leaf is really one of a whorl of four leaves of which three are reduced to small size. Some allied species of *Argostemma* have a terminal whorl of four equal leaves, and in *A. unifolium* it appears that one of these leaves has developed to a large size while the others remain undeveloped.

A few other plants which inhabit these wet rock surfaces beneath the gloom of the forest seem also to have a tendency to reduce the number of leaves and increase the size of one, but in all of these it seems that these are true leaves and that it is only among the Gesneraceae that we find the cotyledons persisting and the true leaves not developed.

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On the Past History of the Ferns.

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With a Diagram in the Text.

UNTIL quite recently the belief has been current that, in the Palaeozoic period, and more especially in Carboniferous times, the True Ferns were sufficiently abundant to form one of the more characteristic groups of the then existing vegetation. Also that, of the two great divisions, the Eusporangiatae were, at that period, by far the most numerous and diversified. In the light, however, of recent Palaeobotanical research on the nature of the fructifications of the Cycadofilices, and other Palaeozoic Fern-like plants, our ideas on this subject are rapidly undergoing considerable modification. The problems connected with the ancestry of modern Ferns have been rendered, if anything, more complex and difficult of solution than before. It is proposed to consider briefly here some aspects of the present position of our knowledge of the Palaeozoic and Mesozoic Ferns.

The point of view adopted will be essentially that of the Geological Record. At the outset, we may distinguish carefully between the problem as to whether a particular race or family was actually in existence during any particular geological period, and the question whether that race had then attained to the position of a dominant[1] or ruling factor in the vegetation of the day. The former is not always capable of solution, but the latter can be answered with confidence in the great majority of cases.

It will perhaps be helpful in this consideration of the ancestry of modern Ferns to approach the Geological Record in a somewhat novel

[1] The term 'dominant' as used here, and in my 'Catalogue of the Glossopteris Flora,' is intended to imply the adjectival sense of 'ruling.' A dominant type is one of several races, which at any particular geological period constituted the more important and characteristic features of that flora. Thus, in the present day flora, among the higher plants, the Dicotyledons, Monocotyledons, Coniferales, and Filicales are the dominant groups.

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manner, and try first to recognize the particular geological period at which one or other of the main divisions of the Ferns attained to its maximum diversity and differentiation, and then to trace it backwards and forwards in geological time, so far as our present knowledge will permit. As the result of comparatively recent research it is now possible to adopt this mode of attack in respect to the more important elements of those floras with which we are best acquainted, i. e. those of the Palaeozoic (Devonian, Lower Carboniferous, Upper Carboniferous, and Permian) and the typical Mesozoic floras of the Rhaetic, Jurassic, and Wealden. If, during any one or more of these periods, one line of descent was particularly successful in the struggle for existence, there is ample evidence of the fact to be found in the rocks of that age in some geographic region or other. The imperfection of the Record, largely exaggerated in the past, can be wholly neglected where we are considering the larger divisions of the Vegetable Kingdom, such as phyla, classes, or groups of plants. For instance, the Cycadean line of descent was obviously at its maximum in Mesozoic times. This is shown by the abundance of Cycadean remains in the rocks of the Rhaetic, Jurassic, and Wealden, in many parts of the world, as compared with the rarity of such fossils in the Palaeozoic and Tertiary (including Recent) floras (see text-figure 1, p. 229).

A study of the broader botanical features of the Palaeozoic and Mesozoic vegetations shows that in the case of a phylum or group which has, at one time or another, been successful, we can often recognize three phases in the line of descent. One such represents the period of the maximum diversity and differentiation, when the race had attained to the status of being one of the dominant factors in the vegetation. The other two, on the contrary, correspond to periods when it was a subsidiary type, and are the stages of adolescence and senility. We can represent these three phases diagrammatically if, instead of indicating by a thin line the record of a phylum or class of plants extending through a number of geological periods, we use a more or less lenticular figure (see text-figure 1, p. 229); the breadth of the figure being proportionate to the degree of differentiation of the group. The broad phase of the life-line indicates the periods at which the race was a dominant factor in the then existing vegetation, the thinner lines, those when it was subsidiary to other groups. No doubt the exact form of the life-figure varies in the case of different races; as will be seen from a comparison of that of the Cycadophyta and the Leptosporangiatae indicated in the text-figure on p. 229.

I propose to attempt to recognize here the various phases in the life-lines of the Modern Ferns. In discussing this problem I have found it helpful, if indeed it is not absolutely essential, to consider separately the lines of descent of the Leptosporangiatae, Eusporangiatae, and Hydropterideae.

The Leptosporangiatae.

When we seek to recognize the dominant phase in the life-history of the Leptosporangiatae, we have fortunately little difficulty. The evidence that, by Rhaetic times, this group had already attained to the status of a dominant factor in the flora is very clear. This position was also maintained in the Jurassic and Lower Cretaceous vegetations.

Of the Tertiary floras our knowledge unfortunately is very vague at present, but the fact that this line of descent is still one of the characteristic features of the vegetation of the world at the present day is proof that the broad phase of the life-line has continued more or less constant through a large number of geological periods. In other words, of the more ancient Mesozoic types, the Leptosporangiate Ferns, like the Coniferales, have on the whole been remarkably successful in the struggle for existence. Even at the present day they still maintain their position as an important element in the vegetation of the world side by side with other races, which attained to a position of dominance at a much later geological epoch.

In contrasting the Fern-like plants of the Palaeozoic and Mesozoic periods, one finds that, so far as their external morphology is concerned, those of the Mesozoic rocks seem to recall the recent Ferns even more closely than one might have expected. It may be admitted that, as regards the general configuration of the fronds, and certain other characters such as the circinate vernation, both the Palaeozoic and Mesozoic representatives agree in being exceedingly Fern-like. But such features are for the most part of little value phylogenetically. Young fronds coiled in a crozier-like manner, often referred to the frond-genus *Spiropteris*, Schimper [1], where their real generic nature cannot be ascertained, are known from the Rhaetic as well as the Carboniferous rocks. In the latter case some have proved to belong to *Neuropteris* [2], others to *Pecopteris* [3]. Among these, the Neuropterids at least were not Ferns, but Pteridosperms. Thus this type of vernation was common to more than one group in past times, just as to-day it is common to both Cycads and Ferns.

There are, however, some features of the Mesozoic Ferns which are sharply contrasted with those of the Fern-like plants of the Palaeozoic. In the earlier Mesozoic Floras, the pedate habit was undoubtedly a characteristic of the fronds of a number of true Ferns. Some of these families, the Matonineae and Dipteridinae, have still representatives living to-day, as Mr. Seward [4] has shown. The type of sympodial branching exhibited by such a Fern-frond as that of the recent *Matonia* or the Jurassic *Matonidium* was not, however, the high-water mark in this direction. In Rhaetic times, as Nathorst [5] has pointed out, we have still more complicated fronds. The

[1] Schimper ('69), vol. i, p. 688, pl. 49, fig. 4. [2] Bunbury ('58), p. 243, text-figure.
[3] Kidston ('01), pl. 26, fig. 1; Potonié ('03), Pl. VIII.
[4] Seward ('99), Seward and Dale ('01). [5] Nathorst ('92), p. 169.

frond of *Camptopteris spiralis*, Nath., for instance, exhibits a combination of the sympodial with the spiral type of branching in a very remarkable manner, a character which is also found, but to a much less extent, in certain leaves of the genus *Dictyophyllum*. Such features are quite unknown among the Palaeozoic Fern-like plants, and although among Mesozoic Ferns the frond is by no means always pedate, the frequent occurrence of this habit is significant.

Similarly the Palaeozoic Fern-like plants exhibit certain features which are more especially their own. Stress has been laid in more than one quarter on the occurrence of the repeatedly dichotomous type of branching[1] found in many Palaeozoic fronds, and especially on the fact that stipular or adventitious outgrowths[2], known as Aphlebiae, occur on the rachis in many cases. I am inclined to agree with a suggestion which was made recently by Professor Oliver that these features may probably be regarded as indicative of the fronds of members of the Pteridospermae rather than of true Ferns.

If, however, we turn to the subject of the fertile fronds of Mesozoic and Palaeozoic age, we are at once struck by the fact that, while such leaves, bearing annulate sporangia often but not always on fronds of unreduced lamina, are almost common in the Mesozoic sediments, such are comparatively rarely found in the older rocks. For instance, to take an example from our best-known British Mesozoic flora, Mr. Seward[3] has described from the Lower Oolite of Yorkshire twenty species, regarded as probably of the nature of Ferns, and in thirteen cases the sporangia are known, which in eight or ten species are borne on fronds practically identical with the sterile foliage, and in three to five others on reduced fronds. Among the Palaeozoic Fern-like plants, the number of species, on the fronds of which annulate sporangia have been discovered, is, by comparison with the total number known, almost infinitely small.

Further it is clear from a study of the fertile fronds of Mesozoic age that, even by the Jurassic period, most of the modern families of ferns had become differentiated. Mr. Seward[4] has recognized members of the Schizaeaceae, Osmundaceae, Cyatheaceae, Polypodiaceae, as well as of the Matonineae and Dipteridinae, in the rocks of that period.

It would be easy to discuss the Mesozoic Ferns at greater length, but enough has perhaps been said to show that, so far back as the Rhaetic period, Ferns belonging to modern families of Leptosporangiatae were not only in existence, but flourishing in sufficient degree to form one of the dominant features in the vegetation of that period.

The Primofilices.

When, however, we try to trace the life-line of the Leptosporangiatae back to Palaeozoic times, we are at once in difficulties. A race which rose

[1] Potonié ('95).
[2] Potonié ('03).
[3] Seward ('00).
[4] Seward ('04), p. 843.

to the position of a dominant factor in the vegetation of past or present times did not spring into existence abruptly, although in some cases it may have reached its dominant phase within a comparatively short geological period. It is true that, in the case of the Angiosperms, their advent certainly does appear to have been remarkably sudden, but one cannot help feeling that this conclusion, however much we may be driven to accept it on the present evidence, is really but the expression of our ignorance on the subject.

Our difficulties, as regards the Leptosporangiatae, are increased by the fact that there exists, at present, a considerable gap in our knowledge. Of all the geological periods from which some of the plant remains are known to us, two are especially interesting in that they represent the most critical epochs in the past history of the Vegetable Kingdom. The earlier of these covers the period in which the change from the Palaeozoic to the Mesozoic facies of plant-life took place. The latter holds the secret of the evolution of the Tertiary-Recent from the Mesozoic facies. How, during this latter period, this transition was effected we know practically nothing at the present moment. Of the earlier epoch, our knowledge is somewhat more satisfactory, but this flora stands in urgent need of correlation and critical revision, and until this has been accomplished, a gap in our knowledge, as I have said, will still exist. So far as one may judge from the present evidence, it would seem that the flora of the Upper Permian and Trias (excluding the Rhaetic) was probably a true Transition flora, in which the older Palaeozoic types gradually died out, and gave place to plants of a newer facies, which quickly rose to the position of dominant types in Mesozoic times. It may be that the thin, subsidiary, incoming-phase of the life-line of the Leptosporangiatae is chiefly to be sought for in the rocks of this transition period, of which at present we know so little. I do not propose, however, to attempt to trace here the evidence of the Leptosporangiate ferns in these sediments. Such will scarcely be possible until the critical revision, above suggested, has been effected.

If we pass back to the flora of the Carboniferous and Lower Permian, can we find any evidence of the Leptosporangiatae, either as a dominant or subsidiary factor in that vegetation? This question is by no means a new one. It has been discussed on many occasions, among them in a paper by Professor Bower[1], published in 1891, in the fifth volume of the Annals. In the course of that contribution, which was in the main devoted to a consideration of such anatomical features of the modern Ferns as bear upon the question whether the Eusporangiate or the Leptosporangiate is the more primitive type of Fern, the author gave some account of the evidence derived from the fossil flora of the Palaeozoic Rocks. He concluded that 'though it is not possible absolutely to deny the presence of Leptosporan-

[1] Bower ('91), p. 127.

giate Ferns in the primary rocks, still the evidences of their occurrence are at least exceedingly rare, and the question whether they existed at all in those early times is not even yet placed beyond the possibility of doubt by observation of microscopic sections.' These conclusions, at that time, were probably regarded as somewhat extreme, at least by those who were more especially concerned with the fossil evidence. At any rate, at the present time we know from more than one source, that annulate sporangia, which, in certain respects at least, may be somewhat closely compared with those of recent Leptosporangiatae, do occur in the Palaeozoic rocks. How far we are warranted, in the absence of any developmental evidence in the fossil state, in referring them to the Leptosporangiate Ferns, is a point which may now be considered in some detail.

The sources of evidence are threefold. In the first place certain impressions of Sphenopterid fronds have been described, sufficiently well preserved to permit of a detailed study of the sporangia which they occasionally exhibit. One of the best known of these, *Hymenophyllites quadridactylites* (Gutbier), the fertile fronds of which were described by Zeiller [1], is generally held to be at least a Leptosporangiate Fern, and very possibly a member of the Hymenophyllaceae. Similarly the fructifications known as *Oligocarpia* and *Senftenbergia*, which are borne on fronds belonging to the form-genera *Sphenopteris* and *Pecopteris* respectively, are among others which appear to be, so far as structureless specimens will permit us to judge, of the nature of Leptosporangiate sporangia. But even if we regard some, at least, of these sporangia-bearing fronds as really Leptosporangiate Ferns, a conclusion which I am inclined to think is probably correct, it must at the same time be admitted that, in point of numbers, such plants were but few in Upper Palaeozoic times, and did not then form one of the dominant groups. I think it possible that, in some of these, we may recognize the beginnings of the thin, subsidiary phase of the life-line of Leptosporangiatae.

In the second place we have more satisfactory specimens, in which the structure is preserved. In both the Lower Coal Measures of England and the Permian of France, the calcareous or silicious nodules are found to contain, here and there, isolated sporangia or sori, for the most part not in obvious continuity with any other organ. Dr. Scott [2] has recently described a striking case in which such sporangia contained spores which had begun to germinate within the sporangium. In this and other examples there is a well-marked annulus [3]. If, however, we closely compare these organs with those of a recent Leptosporangiate Fern, we shall find that they do not exactly agree in certain respects. For instance, as Dr. Scott has pointed out, we invariably find a bi- or multiseriate annulus in these fossils, as

[1] Zeiller ('83). [2] Scott ('04).

[3] Exannulate sporangia also occur, vide Scott ('05).

opposed to the (with rare exceptions) uniseriate annulus of the recent Ferns. In another group, the Botryopterideae, this type of annulus is correlated with other features which are not found in modern Leptosporangiatae. It is better, therefore, to regard these usually detached sporangia with some suspicion as to their exact affinities.

And thirdly we have the evidence, from structure specimens, of the existence of a peculiar family, in Palaeozoic times, belonging to the Fern alliance—the Botryopterideae. The investigations of the late Bernard Renault[1] on these fossils, followed by those of Dr. Scott[2], who was the first to point out clearly the affinities of this group, have shown that, although the Botryopterideae stand nearer to the modern Ferns than to any Palaeozoic group, yet they differ in certain important characters from any known Leptosporangiate Fern. It will not be necessary to enter here into the points of disagreement in detail. It may serve to mention the peculiar nature of the annulus and the fact that the wall of the sporangium is more than one layer in thickness, and to recall the unusual form and the size of the sporangia.

Bearing in mind such differences between these Palaeozoic sporangia and those of modern Leptosporangiatae as have been pointed out above, it would appear to me to be more helpful in our present difficulties with regard to the life-line of that race, as well as more consistent, not to attempt to bring these ancient Fern-like plants into line forcibly with the modern Ferns, however closely we may regard them as allied. Neither the Botryopterideae nor any of these isolated sporangia can be included in any recent family of the Ferns—a conclusion which is not disputed. It would seem much more likely that these fossils formed the only fragments which are at present known to us of an ancient Palaeozoic race. Professor Lignier[3], in a recent contribution, has also come to what I take to be a similar conclusion.

That this race gave rise to the Leptosporangiatae—using that term in the sense applied to the modern Ferns, and here also to the Mesozoic representatives—seems more than probable. Such a suggestion is not by any means new. Dr. Scott[4], in his 'Studies', has clearly pointed out the synthetic nature of the Botryopterideae, 'in so far as they combine the characters of several of the existing families within this division,' i.e. Leptosporangiatae; 'and it is not improbable that they represent the stock from which some at least of the families were subsequently derived.' Mr. Kidston[5] has also arrived at a similar conclusion.

It has seemed to me that it would be convenient if this ancient race, of which, no doubt, the Botryopterideae were but one important family,

[1] Renault ('75).
[2] Scott ('00), chapter ix.
[3] Lignier ('03), p. 103, and footnote; and p. 133.
[4] Scott ('00), pp. 299, 506-9.
[5] Kidston ('05²), p. 162.

were known by some special name. On a recent occasion I suggested the term Primofilices, in view of the fact that such, perhaps preferable, names as Archaeopterideae[1] and Palaeopterideae are not available for this purpose. This term, although not altogether satisfactory, has the advantage of suggesting the Primary or Palaeozoic Age of the race.

One family of the Primofilices has already been recognized (the Botryopterideae), and possibly some at least of the detached annulate sporangia, known from structure specimens, belonged to other representatives. It seems probable that yet further examples will be discovered in the near future. On the other hand, certain of these Fern-like plants may have already begun to specialize along those lines which we see exhibited by the Mesozoic, Tertiary, and Recent Leptosporangiatae, and have thus become virtually members of that group. The evidence of some of the impressions mentioned above suggests that this may well have been the case. If, however, we admit the possibility that the Primofilices were the immediate forerunners of the Leptosporangiatae, the question as to whether Leptosporangiate Ferns existed in the Palaeozoic period becomes of minor importance. The ancestors naturally must be of much greater interest, at the present moment, than the first descendants of a race which we know so well in the living state.

One further conclusion should be borne in mind. Whether we regard the Botryopterideae as an ancient family, from which some of the Leptosporangiatae were later derived, or as a member of that group pure and simple, there can be no doubt that neither the Primofilices nor the Leptosporangiatae were, towards the close of the Palaeozoic period, in the position of dominant or ruling group, as compared with the Pteridospermae, or other of the great phyla, then at their maximum differentiation.

The Eusporangiatae.

When we turn to the geological evidence for the existence of the Eusporangiatae in past times, we have to deal with less trustworthy data. Until quite recently it has been generally held that this group of the Ferns was by far the most abundant and diversified in the Palaeozoic period. As Professor Bower expressed it in his paper, already referred to, 'recent writers have repeatedly remarked the preponderance of Ferns of the Eusporangiate type in primary rocks.' And again, 'where the sporangia have been found, they are in the overwhelming majority of cases of a character allied to the Marattiaceae[2].' In view, however, of the recent discovery by Mr. Kidston[3] of the male organs of *Lyginodendron*, which have proved to be the fossils long known under the name *Crossotheca*, and

[1] The term Archaeopterideae, suggested by Professor Lignier in this connexion (Lignier ('03), p. 103 footnote) cannot hold good, as it is already in use for a Devonian family of Fern-like plants, including the genus *Archaeopteris*.

[2] Bower ('91), p. 122.

[3] Kidston ('05[1]), ('05[2]).

which closely resemble the sporangia of recent Eusporangiate Ferns, this conclusion can no longer be held with the same confidence. How far it will be necessary to modify it, it is impossible to say at present.

We may again approach the problem by attempting to recognize in either the Palaeozoic or Mesozoic floras the broad phase of the life-figure of this race. We may first ask, Is there any evidence that the Eusporangiatae were a dominant group in the Rhaetic, Jurassic, or Wealden vegetations? So far as our present knowledge is concerned, this question can be answered by an emphatic negative. There is no member of these floras which can be regarded, with the least degree of probability, as allied to the family Ophioglossaceae. Further, it is difficult to recall more than a very few species which are or may be assigned to a position in or near to the Marattiaceae. Of these the best examples are to be found in certain fronds of *Taeniopteris*, occurring more especially in the Rhaetic and Liassic rocks.

The genus *Taeniopteris* is a frond-genus, including simple, entire, ribbon-like leaves, often of fairly large size, usually lanceolate or elliptical in form, with a well-marked midrib, and simple or occasionally dichotomizing lateral veins, which pursue a course almost at right angles to the midrib. This type of frond first appears in the Carboniferous and Permian floras of both the Northern and Southern Hemispheres, but it is more especially characteristic of the Rhaetic and other of the earlier Mesozoic floras. It can, of course, be closely matched among living Ferns, a consideration which is, however, of absolutely no value.

In the case of the widely distributed and characteristic Rhaetic species, *Taeniopteris Münsteri*, Goeppert[1], fertile fronds have been discovered. The synangia borne on these fronds have, it must be confessed, so far as one can judge from impressions, a most striking resemblance to those of the modern Fern, *Marattia*. The discovery of such fertile examples of *T. Münsteri* in the Rhaetic rocks of Tonkin, led Professor Zeiller[2] to go so far as to almost place this species within the recent genus. In the case of Swedish examples, which by the kindness of my friend Professor Nathorst I have recently had an opportunity of studying in Stockholm, the resemblance is equally striking.

Another, but in my opinion less satisfactory instance, is to be found in the genus *Danaeopsis*, Heer, and the species *D. marantacea*, Presl[3], from the Triassic of Germany and elsewhere in Europe. The frond of *Danaeopsis* may be roughly described as a pinnate frond, whose pinnae resemble the simple fronds of *Taeniopteris*. Here the synangia are said to recall more closely those of the recent genus *Danaea*, but I am not quite satisfied that this is the case.

[1] Nathorst ('78[2]), p. 48, pl. I, fig. 6 (Höganäs yngre).
[2] Zeiller ('03), p. 63, pl. IX, figs. 6–8, as *Taeniopteris* (*Marattia*) *Münsteri*, Goeppert.
[3] Schimper ('69), vol. i, p. 614, pl. 37.

There is a further impression from the Lias of Poland, named *Danaea microphylla* by Raciborski [1], in which the resemblance to the recent fructification is, perhaps, rather closer.

Thus we find that although there is no evidence to show that the Eusporangiatae were a dominant group in Mesozoic times, there are apparently fairly good grounds for believing that this race was then in existence. But this conclusion, even on the present evidence, would have much greater weight than it appears to me to possess, were it not that there is at least a possibility, as yet to be disproved, that *Taeniopteris* itself may have been other than a true Fern. The suspicion that some of these Fern-like plants, possessing a fructification not unlike the synangia of a modern Eusporangiate Fern, may have been in reality the male organs of members of the Cycadophyta, is at the bottom of our present difficulties with regard to the past history of the Eusporangiatae, as will be seen when we come to discuss possible members of this group in Palaeozoic times. The fact that in the male fronds of the Pteridosperms, and in the same organs of the Bennettiteae [2], a group directly descended from the Pteridospermae, as Dr. Scott [3] has shown, the whole male fructification is strikingly like that of the modern Marattiaceae, cannot be overlooked in this connexion. Also we know that as early as the Rhaetic, some of the Cycadophyta bore seeds, after the manner of the modern genus *Cycas*. The specimen described by Nathorst [4], from the Rhaetic of Bjuf, in Sweden, under the name *Cycadospadix integer*, Nathorst, which I have had the pleasure of seeing recently, appears to me to be conclusive in this respect. If this is so, we should certainly expect to find, among the earlier Cycadophyta, instances in which the male fructifications were not aggregated into cones, but borne on fronds, like the corresponding organs of the Pteridosperms. At the present time, no suspicion attaches to *Taeniopteris* in this connexion, but it is a possibility still to be borne in mind, and one which renders, in my opinion, the otherwise excellent evidence that this genus was a Eusporangiate Fern, rather less conclusive.

We know too little of the transition flora of the Palaeozoic and Mesozoic rocks to justify any attempt to seek for the Eusporangiate line of descent during that period at present. Raciborski [5] has indeed stated that, in the Lunzer Schichten (Keuper) of Austria, the rich flora of which has unfortunately never been worked out, 70 per cent. of the Ferns belonged to the Marattiaceae, but I am not aware of the evidence for this statement. The possibility, however, remains, as I have hinted with regard to the Leptosporangiatae, that a further study of the plants of this transition period may throw important light on the Eusporangiate life-line.

When we turn to the Palaeozoic rocks, we find, as has been stated

[1] Raciborski ('94), p. 13, pl. VI, figs. 1–6. [2] Wieland ('01). [3] Scott ('05[1]), ('05[3]).
[4] Nathorst ('02), p. 6, pl. I, fig. 11. [5] Raciborski ('91).

already, a large number of fructifications which have hitherto been regarded as undoubtedly belonging to Eusporangiate Ferns of the Marattiaceous type. Several of these have been referred to the fronds known under the names of *Pecopteris* and *Sphenopteris*. In some cases the sporangia are free from one another, though exannulate. Such occur on unreduced fronds in *Dactylotheca* (*Pecopteris*), *Renaultea* (*Sphenopteris*), and on reduced fronds in *Urnatopteris* (*Sphenopteris*). Or the sporangia are not only exannulate but united to form synangia. Examples, borne on unreduced fronds of the Pecopteris type, are found in *Asterotheca*, *Scolecopteris*, and *Ptychocarpus*[1]; on reduced fronds of the Sphenopteris type in *Crossotheca*[2].

Less than a year ago Mr. Kidston[3] showed that one of these fructifications, *Crossotheca*, was the male organ of a Pteridosperm (*Lyginodendron*). It is this discovery that has raised the present questions, Are all these fructifications the male organs of Pteridosperms? Did any of them really belong to the Eusporangiate Ferns?

It is obviously hopeless to try to answer these problems at the present stage. There are many indications that the Pteridosperms were a large and dominant group in Upper Palaeozoic times. So far we are acquainted with their male organs in only one case. There is considerable reason to suppose that, among the fructifications mentioned above, others will be found; in fact, it is difficult to imagine where else we are to look for such organs. Also it must be remembered that the male fructifications of the Bennettiteae[4], the direct descendants of the Pteridosperms, were essentially similar to some of these Palaeozoic fructifications, and to those of the modern Eusporangiatae, as I have already indicated. Further, we know from an important discovery by M. Grand' Eury[5] that at least one Pecopterid frond belonged to a Pteridosperm. No doubt *P. Pluckeneti*, among Pecopterids, did not stand alone in this respect. It is, therefore, not unnatural that suspicion should envelop some of the synangia mentioned above, which are borne on Pecopterid fronds.

On the present evidence, I am inclined to think that many others, besides *Crossotheca*, of these Marattiaceous-like, Palaeozoic fructifications will eventually prove to be the male organs of Pteridosperms. All such need not, however, have been of this nature; but at the present moment it seems hopeless to try and distinguish between those which were, and those which were not Pteridospermic[6]. At any rate, there are no longer such strong reasons for believing that the Eusporangiate Ferns were a dominant type of Palaeozoic vegetation.

[1] Figures of these fructifications will be found in Scott's 'Studies in Fossil Botany', and Zeiller's 'Éléments de Paléobotanique'.

[2] Mr. Kidston does not regard *Crossotheca* as consisting of synangia, but of bilocular sporangia.

[3] Kidston ('05[1]), ('05[2]). [4] Wieland ('01). [5] Grand' Eury ('05).

[6] Mr. Kidston ('05[2]), p. 162, however, regards *Asterotheca* as a Eusporangiate Fern, and concludes that, at the close of the Carboniferous period, the Marattiaceae assumed a very important place in this flora.

It may be pointed out in this connexion that we have in the fructification of most of the modern Eusporangiate Ferns, as compared with the male organs of both the Palaeozoic Pteridosperms and the Mesozoic Bennettiteae, an interesting case of homoeomorphy. In each group, the sporangia, though dissimilar physiologically, are all exannulate, and more or less united into synangia, and they were all borne on fronds. Opinions will no doubt differ as to the precise significance attaching to this fact. Some may be inclined to regard it as indicating some degree of affinity between the Fern-line of descent and that of the Pteridosperms and Cycadophyta. Though affinity between these two life-lines at some remote geological period can hardly be doubted, I am not at all sure that this case of homoeomorphy implies a connexion between the Cycadean line of descent and that of the Eusporangiate Ferns in particular. These characteristics in common, though in dissimilar organs, may be simply due to parallelism of development, a frequent phenomenon in both the vegetable and animal kingdoms. Even in the case of organs of similar function in different groups, such similarities may be of little or no value as clues to affinities. For instance, in Palaeozoic times both the Pteridosperms and the Cordaitales, as well as some Lycopods, bore seeds; yet one would not, on this ground, claim that these groups must be nearly related. Exannulate synangia may well be an ancient type of fructification; but it does not follow that the life-line of the Eusporangiatae goes back to any distant geological period, because present members of the group also possess this feature. Thus it appears to me that the argument, based on the similarity of the male fructification of the Pteridosperm to the homosporous sporangium of modern Marattiaceae, can have little weight as a proof of the existence of the Eusporangiatae in Palaeozoic times, using the term in the sense applied to the modern Ferns.

But even if we are inclined to dismiss a large number, but not perhaps all, of the exannulate Palaeozoic sporangia from the Eusporangiatae, there is yet other proof of this line of descent in Carboniferous and Permian times, and one founded on the surer ground of structural anatomy. The well-known and very Fern-like stems included in the genus *Psaronius* are in the details, as well as in the general plan of their anatomy, strikingly like the modern Marattiaceae. A detailed comparison of their structure, as compared with the recent Ferns, on the part of Rudolph[1], has recently emphasized this similarity even more clearly than before. Yet a puzzling feature connected with this type of stem is that certain Psaronii are known to have borne Pecopterid fronds, which in turn possessed an *Asterotheca*-like fructification However, though it may appear difficult to reconcile this fact with conclusions already arrived at with regard to the fructifications discussed above, it may be readily admitted that, in the anatomy of

[1] Rudolph ('05).

the stem of *Psaronius*, we have features which undeniably indicate close affinity to the modern Marattiaceae. To Mr. Kidston[1], who regards *Asterotheca* as above the suspicion of being a male organ of a Pteridosperm, this difficulty of course does not exist.

So far, we have discussed only those Palaeozoic fossils which resemble the modern Marattiaceae. Of the Ophioglossaceae we have, in the Primary rocks, almost as little trace as in the Secondary. There is, it is true, the Permian fossil from Autun in France, which Renault[2] described under the name *Ophioglossites antiquus*, but the evidence for this attribution is extremely doubtful. So far as I am aware, not even a plausible case has been made out at present to show that the Ophioglossaceae occur in either the Mesozoic or the Palaeozoic rocks.

It will be seen, from what has been said above, that the task of tracing back the life-line of the Eusporangiate Ferns to the Palaeozoic period is beset by difficulties. There are at least some grounds for believing, either that they then existed, or that in the Palaeozoic rocks we are dealing with their direct ancestors. Which is the correct view we can hardly decide at present. It may be that in Palaeozoic times the Fern line of descent had not become clearly differentiated into Eusporangiate and Leptosporangiate. Dr. Scott[3] has already suggested that the Botryopterideae combine characters common to the Ophioglossaceae and the Leptosporangiate Ferns. Possibly the origin of the Eusporangiatae is to be also sought for in the group which I have termed the Primofilices, of which the Botryopterideae are the best-known family at present. But until we know more of the exact nature of the Marattiaceous-like fructifications of the Palaeozoic rocks we are hardly in a position to speculate with advantage on these points, or to trace back the life-line of modern Eusporangiate Ferns with any certainty. One fact, however, stands out very clear. The evidence, formerly regarded as beyond suspicion, that the Eusporangiate Ferns formed a dominant feature of the vegetation of the Palaeozoic period, has been undermined, more especially by the remarkable discovery of the male organs of *Lyginodendron* by Mr. Kidston. At the best, we can only now regard them as a subsidiary group in that epoch in the past history of the vegetable kingdom.

The Hydropterideae.

The remaining group, the Heterosporous Ferns, may be briefly dismissed. So far as I understand the evidence, there are no satisfactory grounds, at present, for believing that this race existed at all in Palaeozoic times. I am aware that statements to the contrary are numerous; in fact there exists a small literature on the subject of Palaeozoic Hydropterideae.

[1] Kidston ('05[2]), p. 162.

[2] Renault ('96), p. 30, pl. 82, figs. 7, 9.

[3] Scott ('00), p. 506.

But a close inquiry will show that such evidence as has been brought forward to support this attribution is by no means convincing. The fossils, whose claims to be regarded as members of this group have been so confidently urged by Dawson[1] and Penhallow[2] in Canada, and by Reid and Macnair[3] in Scotland, are, curiously enough, among the oldest plants known to us, for they are derived from Devonian rocks. If the Hydropterideae really were, as has been insisted, a dominant race in that period, it is curious that we meet with no trace of them in the Lower or the Upper Carboniferous floras. But there are other objections, which are much more weighty. It has not, in my opinion, been demonstrated that the fossils, described as sporocarps by Dawson and others, have any real structural resemblance to those of the modern Water-Ferns. It may quite well be true that such bodies as *Parka decipiens*, Flem., are not typical sporangia. But they are not for that reason necessarily sporocarps. Also, in no case has any trustworthy evidence been found as to the nature of the plant which bore them. In some instances they have been attributed to certain stems occurring in the same beds, but it must be clearly understood that the evidence rests entirely on association alone, which in such cases is, by itself, of little or no value. There is also a total absence, among the fossils associated with these obscure fructifications, of plant remains, which could be regarded, by any stretch of the imagination, as in the least similar morphologically to members of the recent Salviniaceae or Marsiliaceae.

In the typical Mesozoic floras there are very few cases in which one would be led to suspect that any of the Fern-like plants should be assigned to this group. Certainly, there are no grounds at present for believing that the Hydropterideae were a dominant race in Mesozoic times. It is not until we reach the Angiospermous floras that we find definite traces of these Ferns. In one case, however, there does appear to be fairly good evidence for the conclusion that we may be dealing with a Mesozoic Water-Fern. The genus *Sagenopteris*, a typical Rhaetic frond, and one which persisted until Wealden times, may have been of this nature. The form of the frond, composed of four leaflets springing from a common petiole, is not at all unlike that of *Marsilia*. In some species (e. g. *S. alata*, Nath.), as Nathorst[4] has shown, the petiole is winged, and thus recalls a feature sometimes seen at the base of the stalk of the leaves of the recent genus. But a more important point is that impressions of fructifications, which certainly do resemble very strongly the sporocarps of the Water-Ferns, are sometimes found in association with the fronds of *Sagenopteris*. In the absence of any known instance in which a fructification of the Lepto-sporangiate type has been observed on the fronds of this genus, this association is distinctly suggestive. However, the affinities of this interesting

[1] Dawson ('86) and ('88), chapter iii.
[2] Dawson and Penhallow ('92).
[3] Reid and Macnair ('99).
[4] Nathorst ('78), p. 85, pl. I, fig. 17; pl. XIX, fig. 4.

fossil must be considered for the present as 'not proven.' At any rate, we have better grounds for regarding *Sagenopteris* as possibly a member of the Hydropterideae, than in the case of any fossil known to us from the Palaeozoic rocks.

We see, therefore, that the Geological Record does not support the idea that the Heterosporous Ferns were, in any sense, an ancient race. On the present evidence, I am inclined to think that they branched off from the Homosporous Ferns, in all probability from the Leptosporangiate line of descent, during the Mesozoic period, with specialization to a hydrophilous habitat. As a concession to the necessities of their new environment they have evolved heterospory, but not that particular type of heterospory which we associate with a seed. In these Ferns we have a new line of development, a distinct type of heterospory, and one which, so far as I am aware, is a much more modern contrivance, in a geological sense, than the seed.

General Conclusions.

The main results which have been arrived at here are expressed diagrammatically in Figure 1. The form of the life-line of the Leptosporangiatae is interesting in comparison with that of the Cycadophyta, which is also shown in the diagram. The absence of any broadening of the life-

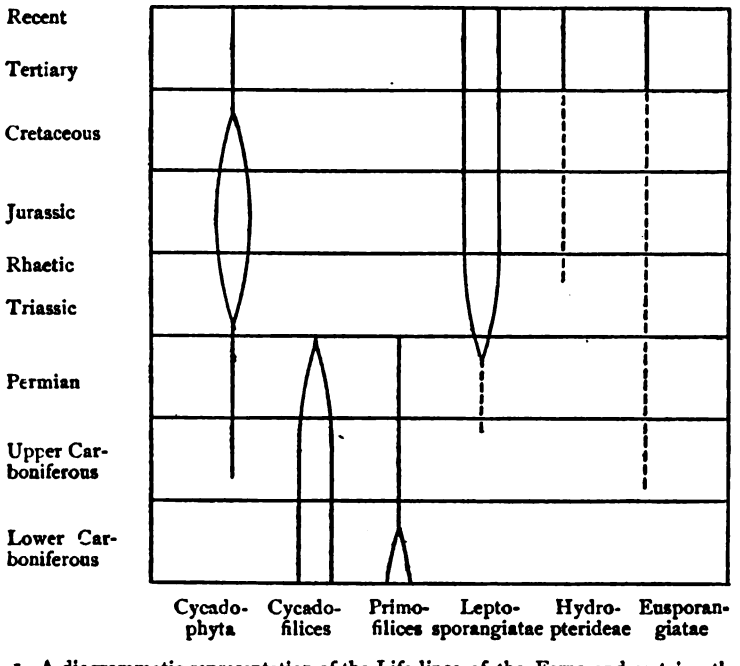

FIG. 1. A diagrammatic representation of the Life-lines of the Ferns and certain other groups, showing the geological periods at which some of them attained to the position of dominant factors in the vegetation.

figure in the case of the Eusporangiatae or of the Hydropterideae, such as would indicate a period or periods when these plants were in the position of dominant groups, is remarkable. The broken lines, in these and other cases, imply that the present evidence for the existence of such groups in certain geological periods is not entirely satisfactory.

As is already generally agreed, the Leptosporangiatae were, in the Mesozoic period, in the position of a dominant group, and most of the families still existing had then become differentiated.

But in the Palaeozoic period it seems doubtful if we can distinguish clearly between two groups, the Eusporangiate and the Leptosporangiate. It is more probable that the members of the Fern alliance, which then existed, although not in the later Palaeozoic forming a dominant group, were really an ancient stock, from which the Mesozoic Leptosporangiatae were derived. For this ancient group, the name Primofilices is suggested, and the Botryopterideae are regarded as being the, at present, best-known family within that group.

As the result of recent research on the nature of the male and female organs of the Cycadofilices, which has tended to show that many of the Fern-like fructifications occurring in the Palaeozoic rocks, formerly regarded as belonging to Eusporangiate Ferns, are more probably the male organs of Pteridosperms, it can no longer be held that the Eusporangiatae were a dominant group in Palaeozoic times. Thus the Geological Record no longer supports the conclusion arrived at by some botanists from a study of the recent Ferns, that the Eusporangiate is the more primitive type as compared with the Leptosporangiate.

The life-line of the Eusporangiatae can only be regarded at present as obscure, so far as the Palaeozoic and Mesozoic rocks are concerned. Even in the latter, little evidence of this race is to be found. Certain fronds of *Taeniopteris* are perhaps the best examples which have been put forward in this connexion, but even this genus is not entirely above suspicion. As regards the Palaeozoic fructifications, formerly regarded as belonging to Eusporangiate Ferns, it is impossible to say at present, which were really of this nature, and which were the male organs of Pteridosperms. Until this can be decided, at least in some degree, it will be impossible to trace back the life-line of the Eusporangiatae with any confidence.

It is pointed out that the male organs of Pteridosperms and the Bennettiteae present a remarkable case of homoeomorphy when compared with the isosporous fructifications of the modern Eusporangiatae. The precise significance of this phenomenon is no doubt a matter of opinion, but it is pointed out here that it may be simply due to parallelism of development.

As regards the Hydropterideae, there are no real grounds for believing, so far as the present evidence is concerned, that they existed at all in the

Palaeozoic period. Even in the truly Mesozoic floras, the only example which can be put forward as a possible representative of this group is the genus *Sagenopteris*, and even here the case cannot be said to be proved.

In conclusion I would express my thanks to Dr. Scott for several suggestions embodied here, and for an opportunity of discussing these questions with him in some detail.

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The Life-history of Bacillus hirtus.

(Synonyms Bacterium hirtum, Henrici; Pseudomonas hirtum, Ellis.)

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With Plate XVI.

INTRODUCTION.

THIS investigation was commenced on the assumption that *Bacillus hirtus* belonged to the genus *Pseudomonas*, because in a former work which I published (1) I found that the ciliation was polar (vide Migula's classification, 11, p. 46). Since then, however, I found that under cultivation, this species became more motile, and when fresh cilia preparations were made the ciliation became peritrich. This was somewhat disappointing because, so far as I am aware, the life-history of the genus *Pseudomonas*, from spore-formation to spore-formation in the next generation, has not been completely investigated. I carried on the work, however, because the only other investigator of this species, Henrici (7), has not given us a full account of its characteristics, and its developmental history is entirely wanting. It was placed by him in the genus *Bacterium* under the name *Bacterium hirtum*, because it appeared to him to be perfectly immotile. But as the following results will show, its motility under cultivation is as great as that of any *Bacillus*, and as its cilia are arranged all round the cell, it belongs to the genus *Bacillus*. As in my earlier investigation of this species (1) cilia were found only at the poles, the question still remains unsolved as to whether under cultivation a cylindrical form of cell may not change its ciliation from polar, to peritrich. The increase in its motility may be caused by that very fact. I propose relegating the solution of this problem to a later investigation. It is important to consider this question for, if true, it would mean that the two genera *Bacillus* and *Pseudomonas* would have to be merged into one genus embracing all the forms at present classed under the two genera. I do not know of a single species at present classed under the genus *Pseudomonas* which has been so long cultivated and in which cilia preparations have been so extensively made, that it can be stated with certainty that its ciliation is polar. I have already shown (2) that non-motile cylindrical forms of Bacteria under cultivation become

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motile, and I think it not improbable that this distinction between *Bacillus* and *Pseudomonas* will, on further investigation, also prove to be non-existent. Against this probability may be set the fact that all spiral forms of Bacteria are undoubtedly polar in their ciliation, and I have satisfied myself in the case of *Spirillum volutans* (*Spirillum giganteum*?) that increased motility on cultivation does not make its ciliation other than polar. It must, however, be remembered that in this genus, the body of the cell continually undulates when it moves, and is not stiff as stated by Migula (11, p. 47), so that this may render the formation of cilia at any place other than the poles impracticable. I may say that, in this investigation, I have taken every precaution to ensure that the form I have investigated was that discovered by Henrici (7) and named by him *Bacterium hirtum.*

The Spores.

The method of examination was as follows. The material was placed in a drop of water, mounted on a coverslip as a very thin layer, and after it had dried, passed through the flame somewhat rapidly in order to fix the spores on to the glass. At the same time, by comparison with unfixed spores mounted in water, care was taken that the size was not materially altered by this process. The dried material was then subjected to the action of stains. In order to ascertain the size of the spores, treatment with stains is necessary, as otherwise the exine cannot be determined with certainty. It is seen at once that the spores are somewhat larger than the average. As the size of the spores of any particular species varies within comparatively narrow limits this should be taken into account in the diagnosis of a species. For *Bacillus hirtus*, the length varies from 1·5 μ to 2·5 μ, and the breadth from 1·0 μ to 1·8 μ.

The size of the spores as compared with that of other species can be seen from the following table, taken from the accurate investigations of Gotheil (6).

	Length.	Breadth.
Bacillus ruminatus . .	1·5–1·7 μ	0·8–1·0 μ
„ *tumescens* . . .	2·5–3·0 μ	1·7–2·0 μ
„ *graveolens* . .	1·9–2·5 μ	1·39–1·7 μ
„ *Petasites* . . .	1·7–2·2 μ	0·83–1·11 μ
„ *ellenbachensis* .	1·7–2·2 μ	0·83 μ
„ *mycoides* . . .	1·4–2·2 μ	0·83 μ
„ *subtilis*	1·7–1·9 μ	0·83–0·94 μ
„ *pumilis*	0·94–1·52 μ	0·55 μ
„ *simplex*	1·39–1·7 μ	0·83 μ
„ *cohaerens* . . .	1·7–2·2 μ	0·83–1 μ
„ *carotarum* . . .	1·31–2·2 μ	1 μ
„ *fusiformis* . .	diameter, 1·3–1·8 μ	

It will be seen that the size of the spore can only be utilized for diagnostic purposes, when it approaches either the maximum or the minimum given in the above table. As the length of the spores of *Bacillus hirtus* is 1·5–2·5 μ and the breadth 1·0–1·8 μ, they rank as very large spores, being surpassed in the above list only by *Bacillus tumescens*.

With regard to the appearance of the spores, this can only be satisfactorily examined by staining, as without any treatment we see nothing except a very strongly refractive oval mass. Fig. 1 shows the spores treated with an Iodine stain. The intine is very clearly marked as a brown peripheral layer forming the boundary of the very strongly refractive contents. The exine, by this method of staining, is somewhat difficult to see, usually only a slight shimmer, radiating on all sides from the spore, is seen. By allowing the stain to act for a somewhat longer period, it becomes visible at last as a faint line surrounding the intine. The intine can be seen more clearly by slightly raising the tube above the focus-point. When the adjustment is very slightly below the focus-point, the whole spore is coloured uniformly brown. The best stains for this purpose are Methylene-blue or Fuchsin. Stained with Methylene-blue (1 c.c. alcoholic sat. solution of Methylene-blue to 40 c.c. H_2O) the spores are more rapidly and more distinctly coloured, and it is not difficult to investigate the structure of the exine. It is seen to be a slightly irregular coat, which at both poles has a somewhat blunt point (Fig. 2). The intine is more distinct, and can be seen still more clearly by very slightly raising the tube above the focus. When the stain has acted for some time the spore becomes permeated throughout. In this condition the intine and its contents contract somewhat, probably due to the effect of the alcohol used in the making of the stain. This brings into prominence the structure of the exine, which does not take part in the contraction (Fig. 3). This stain is to be recommended as the best for this purpose. When stained with Fuchsin (2 c.c. sat. alc. solution, 10 c.c. abs. alc. 10 c.c. H_2O), it was found that after about ten minutes, the exine was sharply brought into prominence. The intine, however, was only seen as a dark line, limiting the strongly refractive contents, but was not coloured. With this stain, as with Methylene-blue, the bluntly pointed ends of the exine are plainly visible (Fig. 4). In Fig. 5 is shown a spore much more highly magnified, which illustrates more clearly its structure when treated with reagents. The spore is thus seen to be an oval structure, with two coats, the inner, delicate and closely wrapped round the contents, the outer a looser somewhat irregular band, to the presence of which is due the resistance of the spore to heat and other injurious influences. When seen 'end on' the spore appears round (Fig. 6). In some cases, especially in unstained preparations that have not been dried on the coverslip, the spores are sometimes seen obliquely. In such cases the spore varies in shape between the circular and

the oblong, but as all parts are not in focus, it appears somewhat distorted. The structure of the spore is therefore normal, and the occurrence of the bluntly pointed ends is common enough to make it not of much value for purposes of diagnosis.

Germination of the Spore.

To observe the germination, the spore-material was sown very thickly over the surface of the Agar in an Agar-tube, which was then placed in an incubator (32″ C.) and examined at various times. Even after three hours some spores had germinated, but the most favourable period for their examination is after 6–7 hours, when a very large number of germinated spores can be observed. This facilitates the task of observing the various stages in the germination. As in all observed cases, the first sign of germination is a swelling up of the whole spore, doubtless due to the absorption of water, with a consequent loss of its very strong refractive power. By observation of Figs. 7–9, it will be seen that the vegetative cell issues from the equator of the spore. I could not observe a single case of polar germination, and believe that equatorial germination is constant for this species. When observed after three hours, in several cases cell-division had already taken place (Figs. 8–9), but in no case were any vegetative cells present, unattended by the spore-membrane. The stages of germination can be seen by comparing Figs. 7–9. First a swelling of the spore, then very soon afterwards a splitting of the exine at the equator take place. Next the young vegetative cell protrudes through the split, and in many cases cell-division takes place (Fig. 8) when the young cell is still attached to the spore-membrane. To observe the further development, the culture was examined after five hours, when a comparatively thick though transparent layer is seen on the surface of the Agar. Cell-division has now proceeded much further in the advanced stages, the spore-membrane has been discarded, and examples similar to those represented in Fig. 10 are comparatively common. In this culture these threads of two-celled individuals were almost exclusively present (an *individual* is distinguished from a *cell* in that no account is taken of any transverse cell-walls that may be present, regard is paid merely to the entity, thus Fig. 9 is an *individual* consisting of two *cells*, Fig. 15 *a* is an *individual* consisting of four *cells*). Even at this stage there is a trembling movement which infers the possibility of movement apart from molecular movement. This subject is discussed more fully under the heading 'Motility.' It is sufficient to mention here that as there are indications of motility even at this early stage, the young individuals soon free themselves from the trammels of the spore-membrane and life in the next generation has begun.

In connexion with the germination of the spores, it would be interesting to know the fate of the intine. Is it cast off with the exine or does

it function as the wall of the newly formed vegetative cell? I have never been able to see any traces of it in germination, and as it forms such a compact covering to the contents of the spore, I am inclined to think that it envelops the young vegetative cell, when it leaves the spore.

Gelatine-plate Cultures.

The appearance on gelatine-plates has been very well described by Henrici (7). A synopsis of this given in Migula's System der Bakterien, Vol. II, is as follows :—'Auf Gelatineplatten sind die Kolonien schon nach 15 Stunden sichtbar: die eingeschlossenen werden zu kleinen, weissen Körnern: die oberflächlichen vergrössern sich zu kreisrunden, flachig angeordneten Scheiben: in der Mitte ist ein dichter, weisser Kern, um diesen eine blassere Zone, dann kommt ein milchweisser Ring, dann eine wasserhelle Zone, und zum Schluss eine trübe Randzone: diese Scheibe, die um 3 Tage einen Durchmesser von 4 mm. besitzt, ist von einem Verflüssigungsringe umgeben. Bei 80 facher Vergrösserung bilden die eingeschlossenen Kolonien unregelmässig runde graue Scheiben, die durch abwechselnd hellere und dunklere Stellen ein fein zerklüftetes Aussehen erhalten; allmählich werden sie dunkel und undurchsichtig und der anfangs glatte und scharfe Rand bildet ein Gewirr kurzer Fäden. Die oberflächlichen Kolonien erscheinen zunächst als unregelmässig geformte, graue Scheiben, die von verworrenen dunklen Linien durchzogen sind; vom Rande laufen breitere oder schmälere, bald längere, bald kürzere, zickzackförmige, blitzähnliche Auswüchse aus; allmählich wird das Bild regelmässiger; entsprechend der schon mit freiem Auge wahrnehmbaren zonigen Anordnung sieht man eine kreisrunde, graue, aus einem bald dichteren, bald lockeren Fadengewirre bestehende Scheibe, von deren Rande ein Gewirr kurzer Fäden borstig absteht. Die am Boden flach ausgebreiteten Kolonien zeigen ein den oberflächlichen ähnliches Bild.' This description agrees in the main with the appearances presented by this form, but as the growth on gelatine-plates is notoriously inconstant, and as in the identification of species much stress is laid on growth on gelatine, we have to be certain that the characters that are laid down as distinguishing marks are really constant. Thus the exact composition of the gelatine, its mode of preparation, and more especially the amount of water present influence the appearance of colonies to a very considerable degree, and it is probable that this inconstancy in the shape and form of these colonies is the reason why there is such an apparent multitude of species. Over a thousand species have been described belonging to the genus *Bacillus* alone. It seems to me that a somewhat more elaborate and painstaking investigation would considerably reduce the number, as a very widely distributed

organism like *Bacillus subtilis* must have appeared, I have no doubt, under a dozen different names.

In all cases, growth on gelatine-plates begins to be apparent by the appearance of minute greyish-white specks, both on the surface of the gelatine as well as beneath the surface. The latter colonies do not proceed much further. The superficial colonies, however, are round, have sharp contours, and each colony appears denser in the middle than at the sides, because owing to abundant growth the middle part is raised more above the surface than is the peripheral growth. It often results in the appearance of a 'nucleus' at the centre of a colony. Again, as a peptonizing ferment is present, the appearance of the edge of the colony begins to alter, and as described by Henrici, the beginning of liquefaction is the cause of the various strata which the colonies exhibit, the one furthest from the centre being of course the most transparent. Again, the colonies have at first sharply defined edges, but later become irregular and often exhibit 'blitzähnliche Auswüchse.' It must not be expected that these outgrowths invariably occur, and as a matter of fact in about 50% of the gelatine-plates they are absent. It depends on the constitution, density, dryness, &c., of the gelatine whether they occur or not. Again it must be borne in mind that many other Bacteria possess the same characteristics. Another point which should be noticed is that the relation between time and the size of the colonies is by no means constant. The growth on Henrici's gelatine-plates was extremely rapid: in all those which I made I did not obtain a quarter of the growth mentioned by him, though ultimately as large and larger growth was obtained when the colonies were not too crowded. The following results show the relation between size and time in a few instances. They were not all made at the same time of year, hence as the temperatures were necessarily different, another factor is introduced. It suffices to show that for any given form no constancy in this respect can be expected.

I. Minute specks after eight days, which after fourteen days showed a diameter of 1·5–2·0 mm.

II. Minute grey colonies after three days, which became very thick and granulated and completely liquefied the gelatine in thirteen days.

III. Minute grey colonies after two days. Gelatine completely liquefied after nine days. In this experiment the plates were placed on top of an incubator (32″C.), and were therefore slightly warmer than the surrounding atmosphere.

Other experiments, not recorded, showed the same variations in the growth and liquefaction of the gelatine.

The following are not to be depended upon, in diagnosing a species by means of gelatine-plates.

1. Any relation between size of colonies and time of growth.
2. Any relation between time and liquefaction of the gelatine.
3. Any diagnostic characters based on irregularity of growth of the colonies.

With regard to No. 3, the round or oval form of the colony is often departed from, and even in the same plate there is often considerable diversity of structure. The chief external factors which influence the growth on the gelatine are the following :—

1. Temperature.
2. Crowding or otherwise of the colonies.
3. Percentage of water in the nutrient gelatine.

With regard to *Bacillus hirtus*, under all circumstances, the colonies are first noticeable as minute grey specks, which in course of time liquefy the gelatine. In addition it may be stated, that usually the colonies become extremely irregular, and that very often the superficial colonies show a granulated appearance and vary in thickness from the centre to the periphery, the thickness being greatest at the centre and least at the periphery. In most cases this results in the formation of a 'nucleus' at the centre, leading down to the periphery by means of stratified layers. Less often growth is characterized by the formation of irregular threads or bands stretching out from the surface, which is well described by Henrici as 'blitzähnliche Auswüchse.'

Agar-plate Cultures.

A culture was made from an inoculation taken from a growth in an Agar-tube which was one day old. After fifteen hours at 32° C. there was a splendid growth. The superficial colonies ranged from mere specks up to the diameter of 1 mm. The larger colonies were well raised from the surface and white in colour. Under the microscope (× 80) each appeared as if made up of threads densely packed together. At the edge a clear transparent line bounded the colony. Under higher magnification, the individuals are seen to be motile, and almost invariably consisted of two cells joined together as in Fig. 11, evidently indicating that all the cells were rapidly dividing, and that separation took place as soon as the wall had been formed. I take this to be the surest sign, that the conditions of growth are very favourable. In this culture every individual was motile. The demonstration of the cilia is given in the paragraph on the motility of this form. The colonies under the surface were much smaller, uniformly opaque with a ragged edge, sometimes thrown out into jagged promontories. After twenty-four hours, some of the colonies were from 2–2½ mm. in diameter, and very much raised from the surface. As they get bigger they often lose their round outline, becoming somewhat wavy. If the growth on the plate has been very

rapid, or if the colonies were planted too close together, the whole plate becomes suffused with a uniform homogeneous layer, and often this homogeneous layer is the first indication of growth that is obtained. In this particular culture I saw the most prolific formation of spores that I have ever witnessed. Every available spot had been used up for this purpose. In some cases, some of the individuals had lengthened without dividing: in these, the spores were arranged very close together, often as many as 6–9, so closely packed together that the cell would have found it impossible to find room even for another half spore (Fig. 12). It thus seems as if, in the case of *Bacillus hirtus*, a plentiful supply of oxygen influences favourably the formation of spores. The formation of spores, however, must be due to more than one factor, for in another Agar-plate which I set, under approximately the same conditions, there were no spores, but all the individuals were extremely motile. After forty-eight hours, however, the motility had been lost, and spore-formation had commenced. It was not, however, as profuse as in the former culture. It will be seen later, that in an Agar-tube growth the formation of spores usually takes place after three days, so that the conditions under which growth takes place in an Agar-plate expedite the formation of spores. I consider that spore-formation is the result of the sum total of at present unknown external circumstances. In order to test the effect of the absence of oxygen on spore-formation, cultures were grown in Buchner's anaerobic tubes. Apparently the formation of spores was not influenced by the absence of air. This subject was not pursued any further, as it was beyond the scope of this investigation.

There are two characteristics of *Bacillus hirtus* Agar-plates, which, though not invariable, yet may help in diagnosing the species. The first is that, as was pointed out to me by one of my students, Mr. Pettigrew, the Agar often appears partially liquefied. It never extended so far as to liquefy completely the whole of the medium, but a distinct liquid film was formed on the surface, after which growth and also liquefaction appeared to cease. It is probable that a ferment was secreted which dissolved the Agar, but that later other secretions acted as a deterrent to further action of the ferment.

The second characteristic is that occasionally the Agar-plate cultures take on a deep bronze colour. When the colonies are first formed, they possess the normal white colour, but occasionally the deep bronze colour appears. The conditions of the formation of this development were also not further investigated, but it is probable that slight peculiarities in the constitution of the Agar may have contributed to this peculiar growth. When I inoculated from a bronze colony on to an Agar-tube, I found that at first a fleshy crinkled white growth appeared on the surface. This, after three days, assumed a bronze colour at the top, which gradually

encroached on the white, till after ten days the lower half was white and the upper half bronze-coloured. This fleshy crinkled growth in this species is not normal for growth in Agar-tubes. Microscopically there was nothing remarkable except a diminished formation of spores. As a matter of experience I have found that a fleshy growth is almost always associated with a diminution or absence of spore-formation in those forms which habitually form spores. With regard to the bronze-coloured colonies and bronze-coloured Agar-tube cultures, they retain their colour for at least a year, but when inoculated into a fresh tube, the colour of the new generation is again normal.

Gelatine Stab-Cultures.

It is as useless giving any particulars of the rate of growth of a gelatine stab-culture for diagnostic purposes as for a gelatine plate-culture, for having made them at different times of the year, using tubes which necessarily did not belong to the same preparation, I have never obtained uniform results. Henrici records a rapid growth. In my cultures growth was oftener extremely slight. In Fig. 13 is shown a drawing of a gelatine tube after three months. Fig. 14 shows another gelatine stab-culture only three days after inoculation. The liquid part had a yellowish-brown colour, was turbid, and had a thick deposit at the bottom of the liquid. Lower down, the continuation of the stab showed a few small round colonies each with fine radiating branches. In a few days after this the gelatine became completely liquefied. In a third experiment, about half the gelatine had become liquefied only after two months. In all cultures a constant feature was the appearance on the surface of a light grey speck. Sometimes it increased rapidly in size, but oftener growth was exceedingly small. Along the stab there was a very scanty growth, showing its strong aerob tendency. The surface growth extends into a roughly circular greyish-white covering on the top of the gelatine. At some time or other liquefaction always sets in, provided that the organisms are still alive. Usually the liquefied part has, in suspension, a very fine flocculent greyish-white precipitate. If growth proceeds filter-fashion as in Fig. 13, there is a thick sediment at the bottom of the filter-tube. The same happens when the whole of the gelatine has been liquefied. I examined the individuals of a gelatine tube, in which the gelatine had taken four months to liquefy completely, and found them perfectly healthy, but there was no spore-formation.

Growth in various Liquid Media.

As a further help in diagnosing this species various liquid media were prepared, because Bacteria in the assimilation of N and C differ in the mode of combination of these substances which best suits them. The various

media were taken from Meyer's list, mentioned in Gottheil's work (6). The media were inoculated from spore-material and incubated at 31°–32° C. For the sake of uniformity I have numbered these liquid media in the same manner as Gottheil (6). No. II is not easily available, and I have therefore discarded it.

O. Lemco 1·0 gram.
Peptone 1·0 „
Cane-sugar 0·5 „
Dextrose 0·5 „
Milk-sugar 0·5 „
Seignet salt 0.1 „
Water 120 c.c.

V. Asparagin 1·0 gram.
Glycerine 1·0 „
Cane-sugar 0·5 „
Mineral soln. 100 c.c.

V. Asparagin 1·0 gram.
Milk-sugar 3·0 „
Mineral soln. 100 c.c.

VI. Ammonium tartrate 1·0 gram.
Glycerine 1·0 „
Cane-sugar 0·5 „
Mineral soln. 100 c.c.

VIII. Pot. nitrite 0·05 gram.
Soda 0·5 „
Mineral soln. 100 c.c.

X. Asparagin 1·0 gram.
Dextrose 3·0 „
Mineral soln. 100 c.c.

I. Lemco 1·0 gram.
Peptone 1·0 „
Cane-sugar 1·0 „
Water 100 c.c.

III. Peptone 1·0 gram.
Mineral soln. 100 c.c.

IV. Asparagin 1·0 gram.
Mineral soln. 100 c.c.

V. Asparagin 1·0 gram.
Cane-sugar 3·0 „
Mineral soln. 100 c.c.

Vβ. Asparagin 1·0 gram.
Galactose 3·0 „
Mineral soln. 100 c.c.

V. Asparagin 1·0 gram.
Glycerine 1·0 „
Mineral soln. 100 c.c.

VII. Pot. nitrite 1·0 gram.
Cane-sugar 0·5 „
Glycerine 1·0 „
Mineral soln. 100 c.c.

IX. Dextrose 0·5 gram.
Cane-sugar 0·5 „
Mineral soln. 100 c.c.

XI. Ammon. sulphate 0·25 gram.
Sodium carbonate 0·5 „
Mineral soln. 1000 c.c.

MINERAL SOLUTION.

Potassium phosphate 1·0 gram.
Calc. chloride 0·1 „
Magn. sulphate 0·3 „
Sod. chloride 0·1 „
Distilled water 1000 c.c. + a trace of iron.

In the appended table + + + indicates strong growth. + + weaker growth. + still weaker. o no growth.

The following table shows the results of inoculations in these media.

	O.	I.	II.	III.	IV.	V.	V.	Vβ.	V.	V.	VI.	VII.	VIII.	IX.	X.	XI.
	+ + +	+ + +	not tried	+ +	o	o	o	o	o	o	+ +	o	o	o	o	o
Reaction	acid	acid	—	alkaline	—	—	—	—	—	—	acid	—	—	—	—	—

Fischer (4, p. 55) in speaking of the N and C requirements of Bacteria, says :—'Nicht brauchbar als Kohlenstoffquelle sind Harnstoff, Oxalsäure, d.h. diejenigen, deren Kohlenstoff unmittelbar mit Sauerstoff verkettet ist, und ebenso Cyan, die Stickstoffverbindung. So hat es den Anschein, als ob der Kohlenstoff am brauchbarsten sei, wenn er nur mit Wasserstoff verbunden ist, also als CH_2, weniger gut als CH, noch minderwertiger als CH.OH und gar nicht als CO und CN. Eine ganz glatte Skala hat man hier freilich nicht vor sich.'

So far as O, I, and III are concerned it is impossible to say how the C atom is arranged. In the others the C atom is attached in all the ways mentioned by Fischer, but capacity to grow in any particular medium is not, it seems to me, such a simple affair that it depends upon the mode of attachment of the C atom. The sum total of conditions must be favourable, and what these are we at present do not know.

The growth on No. I affords a diagnostic property which I have never known to fail, though I have made a large number of cultures in this medium. About the third day (sometimes sooner) a white pellicle forms on the surface. It is composed of non-motile individuals, and when first formed is devoid of spores. The spore-formation, however, is only postponed. After six days there are still usually no spores present. In a four weeks old culture, however, it will be found as a general rule that spores are quite abundant. I have always used this medium for accelerating the motility of sluggish cultures, and for initiating motility in cultures which, owing to their previous habits (in the laboratory, not in nature), had not when examined a trace of motility. The cells are of normal breadth and have dense contents. The short threads are very actively motile, the longer ones less so, doubtless owing to the fact that there is more inertia to overcome. The appearance of some of the longer threads is shown in Fig. 15, though it must not be inferred that this formation of threads is a constant feature; the only constant characteristics are (1) formation of pellicle, (2) acid reaction.

The growth in Nutrient Medium O is naturally much similar to that in Nutrient Medium I. In this case there always appeared an extremely thick sediment at the bottom of the culture and a pellicle similar to that on No. I on the top. The formation of spores was very scant. After thirteen

days the threads had somewhat lengthened, thus showing signs of a want of health, but a very large number were still actively motile. It is probable that an abundance of food-supply has acted as a deterrent to spore-formation within the first six to seven days, and that later it has become impossible owing to the abnormal amount of excreted matter consequent on the postponement of spore-formation beyond the normal three days. The constant characteristics are (1) formation of pellicle, (2) strong acid reaction, the reaction in this culture being stronger than that in No. I.

The growth in No. III is weaker than in Nos. O and I, evidently because the organism has to obtain its carbonaceous as well as its nitrogenous supply from the peptone, so that it evidently suffers from a disadvantage. When examined after eight days, the colourless nutrient medium had become turbid with a large number of suspended particles in solution. As was the case with the others, a pellicle was formed on the top. Spore-formation was wanting and there was a precipitate at the bottom, only in this case the precipitate was somewhat gelatinous in appearance. The culture showed, as was to be expected, a tendency to form long filaments, apparently as before, due to the fact that whereas the organism has sufficient energy to extend in length, it had not sufficient to carry out the process of division. When, however, short cells had been formed, these were invariably motile. The reaction was strongly *alkaline*, which should be a good diagnostic for the identification of this species. The constant characteristics are (1) formation of pellicle; (2) gelatinous precipitate; (3) strong alkaline reaction.

The growth in No. VI is similar to that in Nos. O and I. Here also we see a tendency to form filaments, an absence of spores, a pellicle on the surface, a slight sediment at the bottom and a turbidity in the liquid. The reaction is acid. All these which have just been mentioned are constant. It will be observed that the source of N in this case is ammonium tartrate $\left(\begin{matrix}CH.OH.COONH_4\\ |\\ CH.OH.COONH_4\end{matrix}\right)$. It will also be observed that this is the only successful medium, of those tried by me, in which the chemical composition is known. The availability of the C cannot depend on the combination CH . OH, for the same combination is obtained in several of the other media. In others, e. g. those in which asparagin is used, we have the combination CH, which is supposed to be still better, and yet no growth has taken place in Nos. IV, V, Vα, Vβ, Vγ, Vδ, in all of which asparagin is present. As mentioned above, I do not think that the question lends itself to an easy explanation, and the sum total of the conditions in each case must be considered.

GROWTH ON DEXTROSE-AGAR.

I have examined in detail the growth of this organism on Dextrose-Agar, from spore-germination to spore-formation in the next generation, in order to obtain a general idea of its life-history. The Dextrose-Agar was made up of the following materials: Agar, 1·6 grams; Dextrose, 1·0 gram; Na, 0·2 gram; Lemco, 1·8 grams; Peptone (Witte), 1·2 grams; Water, 100 c.c. In all cases growth commenced from the spore. This was effected by heating the spore-material for two minutes in boiling water, which thus killed off the vegetative cells but would not appreciably diminish the germinating power of the spores. The spore-material was placed in a drop of sterile water, contained in a small sterile test-tube. The latter was then immersed in the boiling water. After heating the spores were sown over the surface of the nutrient Agar and then incubated at 32°C.

Germination.—The details of germination are given above.

After fifteen hours.—The appearance of the culture after fifteen hours varies considerably. Sometimes rapid growth has taken place, which is marked by the appearance of a light grey, somewhat transparent layer. Sometimes, however, the growth has been slow, and it is only by holding the culture up to the light that it is seen that growth has taken place; a filmy covering is seen which is very transparent. At this stage almost all the individuals are either 1-celled (Fig. 16) or 2-celled (Fig. 17) and very motile. The motility is of five kinds.

1. A forward movement accompanied by a violent wriggling of the whole body.

2. A forward movement accompanied by a fairly rapid oscillation in which the centre of the cell is the fulcrum.

3. Rotation.

4. A forward followed by a backward movement along the same direction, or else a sharp turn in another direction.

5. Violent trembling of the whole body unaccompanied by a forward movement.

In fact all the varieties of motion which can be observed in a member of the genus *Bacillus* can be seen in a fifteen hours old culture of this species, provided that growth has been favourable. *After twenty-four hours* no great change has taken place in the appearance of the individuals as seen under the microscope, although there is usually a far thicker growth on the surface of the Agar. This takes the form of a somewhat light grey layer, the commonest of all colours on Agar cultures. The individuals were examined by means of the stains, Iodine, Methylene-blue, Bismarck-brown, and Fuchsin, all of which serve their purpose very well. The intimate structure of the cell is discussed in the section dealing with the cell-contents.

In a two days old culture the light grey covering is continued so as to form a pellicle on the surface of the condensed water. This formation is

never wanting. Microscopically the presentation is almost the same as in a one-day-old culture, except that there is a slight increase in the number of 2-celled as opposed to 1-celled individuals. This is to be expected in an older culture for, as stated above, there is present a larger amount of excreted matter which cannot but be unfavourable to growth, and in addition the amount of available food which can be drawn upon must be far less than it was twenty-four hours previously. In most cultures of this age there is no sign of spores, though sometimes cultures pass through the stages of growth very quickly and some individuals have begun to form spores even after two days. The motility is unabated, and as is seen in Fig. 18 the cilia have the peritrich arrangement characteristic of the genus *Bacillus*. There is no appearance of degeneration in the cells, as the cytoplasm always presents the same dense appearance in all the cells, when stained with the usual colour-reagents. I find Methylene-blue to be the best for this purpose, as when a dead cell is stained with it, not only is its cytoplasm very much less densely stained than that of a cell which was alive when treated with Methylene-blue, but the colour alters appreciably, changing to a more purple hue. At this stage the number of dead cells is extremely small. *In a three days old culture*, a great change has usually taken place. If the culture be normal, almost all the individuals are beginning to form spores, and very many of these spores have the glistening appearance peculiar to mature or nearly mature spores. The motility is unchanged in those individuals in which spore-formation has not taken place, and very often the individuals showing spores are also motile. Usually, however, the latter have come to rest indicating that a loss of ciliation has occurred due to the withdrawal of cytoplasm, in order to supply the spore, but motility remains in those individuals in which the demands of the spore have not exhausted the cytoplasm of the cell, for it is evident that an independent thread of cytoplasm like a cilium cannot remain functional apart from the cytoplasm of the interior of the cell, and if the latter be used up to form a spore, the detachment and consequent falling off of the cilia must inevitably take place. I have demonstrated in a former paper (3) the manner in which the cilia penetrate the cell-walls and establish continuity with the cytoplasm inside the cell. In Fig. 19 is shown a case in which spore-formation has not completely exhausted the cytoplasm, and these must be the individuals which, whilst forming spores, do not lose for the present their motility. As regards the non-sporing individuals, their structure does not differ from that of individuals taken from one-day and two-day-old cultures. At this stage a certain number of individuals have been cut off in the struggle for existence, and when stained with Methylene-blue, or any of the other stains, indicate their condition by the weakness of the colouring, and with Methylene-blue, as was mentioned above, by a change in colour as well.

In the case of individuals in which young spores are present, the cytoplasm still stains deeply, but in most cases when the spores are fully ripe, as explained later, the cytoplasm stains only very lightly. In normal development, the number of spores entirely free from the vegetative cells which formed them is very small, though if the culture be well advanced the number may be considerable.

In a four days old culture there will usually be seen free swimming vegetative cells without spores, spore-containing individuals which may or may not be at rest, and free spores. If the culture be well advanced the number of free spores will greatly preponderate, and in many cultures of this age scarcely anything except free spores is to be seen. In some cultures, however, there may be very few spores formed. It is difficult to account for this, for there is no apparent difference between these cultures and those in which spore-formation has been very active either in appearance or in the conditions of growth, but probably an important factor is that the amount of excreted matter is less in the latter case, thus not preventing the normal development of spores. In non-sporing cultures it is noticeable that the vegetative growth is much greater, which naturally infers a greater quantity of excreted matter. On the other hand it is remarkable that by withdrawing a culture from its own excretion products by reinoculating into another tube it is possible to postpone the formation of spores, so that it seems as if both the absence of excretion matter and the excess of it are detrimental to spore-formation. It seems as if unfavourable conditions, e.g. the presence of much excreted matter, induced a tendency to form spores in normal cultures, but if the unfavourable conditions had gone too far, that the organism was not able to do this. There are doubtless other factors which influence the course of the life-history, but at present they are very insufficiently worked out. The same remarks apply to the motility of four-day-old, as to three-day-old cultures, i.e. the motility is dependent on the spore-formation. In Fig. 20, which was taken from such a culture, it will be seen that some individuals are still in the same condition as those in one-day-old cultures.

From now on, no change takes place in the appearance of the growth on the surface of the Agar, except that due to the gradual evaporation of the water and the consequent drying up of the nutrient medium which slightly alters the appearance of the surface growth. The course is now complete and no further change takes place till the spores, finding the necessary conditions of temperature and moisture, begin the cycle once more by germinating.

Cell-Division.

Migula, in his System der Bakterien, p. 140, makes the following assertion with reference to the mode of division of the cells of Bacteriaceae: 'Gegenüber den Coccaceen ist diese Teilung dadurch charakterisiert, dass ihr eine zur Teilungswand senkrechte Streckung der Zelle vorhergeht. Es ist hier also ein entwickelungsgeschichtliches Merkmal gegeben, durch welches die Coccaceen scharf von den übrigen Bakterien getrennt werden.' My observations confirm this statement so far as the majority are concerned. In most cases, the individual showing two cells, in which the division wall is not fully formed, is longer than any one-celled individual. This, however, is not universal, as is seen in Fig. 23 where division has taken place without previous elongation, and in Fig. 24 is shown a case where very slight elongation has preceded the act of division. Hence, though Migula's statement is true for the majority, its application does not appear to me, from my observations, to be universal. All we are entitled to assert is that elongation in length preceding division is much more common in the Bacteriaceae than the converse process, and we may also assert that this precedence of elongation is much more common than is increase of volume preceding the division of the Coccaceae. The two orders cannot be absolutely distinguished by this characteristic; all we are entitled to say is, that in one order one kind of division is much more common than it is in the other.

The second point to determine is whether a division-wall is formed before or after the constriction at the point where the wall appears. Meyer (9) figures a case (Fig. 9 *d*) in which there appears to be a very slight constriction preceding the formation of the division-wall. I have not noticed this stage in this Bacillus, and in another form of Bacillus, in which I was able to follow the division from beginning to end, no constriction was to be seen preceding the appearance of the division-wall. I was able to observe a single cell dividing, and then the daughter-cells repeating the process, until the genesis of more than a hundred individuals from a single cell had been directly observed: in this case the daughter-cells remained attached, so that I was able to observe the process of division several times over. In no case did a constriction precede the formation of a wall. If this were the usual mode of procedure, it should not be difficult to find stained specimens exhibiting this stage in the division, but I have never been able to see this stage in any of my stained preparations. On the other hand, by careful staining, numerous cases are seen in which individuals without the slightest constriction possess division-walls (Figs. 9, 11, 17, 30). The method of staining, which gave the best results with me, consisted in treating the cells with about 50 % Formalin for 3–4 minutes, then adding to the liquid by means of a platinum-loop, two or three loopfuls of a somewhat dilute

solution of Fuchsin or Methylene-blue. The exact amount to be added can easily be ascertained after a little experience. The division-wall is seen as a very narrow band stretching across the cell, perpendicular to the long axis of the cell (Fig. 24). It appears to stain less intensely than the mature wall, when it first makes its appearance, but this may be due to an optical effect, the result of its narrowness. The next stage in the process is the formation of the constriction (Fig. 25). Two processes now seem to go on concurrently, the extension of the constriction and the partition of the division-wall. In some cases the constriction proceeds so quickly that the cell is already half cut off before the division of the wall has taken place (Fig. 26). In other cases division of the wall has taken place before the constriction has advanced a third of the way across (Fig. 27). The new transverse wall is divided by a clear space running longitudinally across the division-wall (Figs. 26, 27). The latter at this stage is seen as two very thin lines, one on each side of the clear line, and by their narrowness easily distinguishable from the wider, more deeply staining walls of the rest of the cell. This clear space is due to a mucilaginous change in the composition of the division-wall, at the place where a clear space is seen. There is no doubt that for some time there is at this stage protoplasmic continuity between the separating cells, though it cannot be demonstrated at this stage of the division. The next stage in development after the appearance of the thin clear line consists in the gradual strengthening of the new wall, with a concurrent rounding off of the end, until ultimately the constitution of the division-wall is not distinguishable either in density or in breadth from the remainder of the wall (Fig. 28). When two dividing cells have reached this stage they gradually draw away from each other, though they are often still connected. Sometimes two cells which have separated and are half a length apart move and wriggle about as if a rope connected the two. And such in fact is the case. In Fig. 29, stained by Grain's method, the union between the cells by means of a protoplasmic cord is evident. In Figs. 30–34 are shown on a larger scale the stages in the division of the cell, showing the two different ways in which the final stages in the division are completed.

With regard to the time required for the whole process of division to take place, Meyer (9) asserts that in one of his observations an hour elapsed between the appearance of the division-wall and the formation of a definite constriction. It is natural to expect that there will be great variation in the rate, but in nature the process must, under favourable conditions, take place at a much faster rate. In one experiment which I made in connexion with this point a one-cell individual divided up until, roughly speaking, about 128–140 cells had been formed. This represents the seventh order of division. To form these cells about three hours were required in this particular instance. I could not follow it further because

the whole mass suddenly separated into its component parts, and each individual began a separate existence. This naturally caused them to disappear from the microscope-field. From the data here supplied, the time necessary for a single complete division from beginning to end was

$$\frac{3 \times 60}{7} = 25 \text{ minutes.}$$

If we bear in mind how short a time it takes for an Agar surface to be completely covered with a thick growth when it has only been inoculated at a single point, it must often happen that a complete division takes place in less time even than twenty-five minutes.

Development of Spores.

To observe the formation of spores, material was taken from a three days old culture, in which, as a general rule, a number of spores of all ages is seen in the microscope-field, and there will usually be a large number of individuals showing the early stages of development. Meyer's stain (10) given for nuclear coloration does very well for the first stages of spore-development, but it is necessary to modify the method, so far as the quantity of stain to be used is concerned. The method which I employed consists in fixing the material for three or four minutes in a drop of Formol, then staining by adding to the Formol a few loopfuls of a solution made up as follows:—

2 c.c. alc. sat. solution Fuchsin.
10 c.c. abs. alc.
10 c.c. H_2O.

Sometimes it will be found advisable to dilute the Formol with water. With regard to the number of loopfuls of the stain which will be required, that must be tested in each individual case: sometimes good results are obtained by using four or five loopfuls to the drop, and examining after four minutes. At other times, especially when the drop is comparatively small, we can use less of the stain, and examine after a longer interval. Again, results quite as good can be obtained by using other stains, e.g. Methylene-blue. A good stain can be obtained by mixing 1 c.c. of a saturated alcoholic solution of Methylene-blue and 40 c.c. of water. Care must be taken that the drop containing the material does not dry up, otherwise accurate observation of young spores is impossible. The first stage in the development is seen in the formation of a clear oval area in the interior of the cell (Fig. 35). This space is of the same size as the mature spore, and represents, as it were, the site that will be occupied by it. This space is clearly marked off from the surrounding cytoplasm, but this depth of staining does not differentiate the cytoplasm from the wall. In one instance I observed 12–15 cells attached together, all of which were at this stage of development. In each

clear space a round spot was visible, from which in one or two cases slight radiations were observable (Fig. 36). This I take to be the nucleus, surrounded by cytoplasm, which thus makes it a fairly prominent object. I did not see a single case in which more than one of these round objects was visible, and the method of preparation of the slide precludes the idea that they are artificial products. They are not always found at the centre (Fig. 37). In Fig. 38 we see two examples of this stage in the same individual. It seems, therefore, that the first stage of development in the formation of the spore consists in the withdrawal of the bulk of the cytoplasm from a clear space. In this space is found a nucleus, which is surrounded by a thin film of cytoplasm, and connected to the cytoplasm surrounding the clear space by thin strands of cytoplasm. Fig. 39 represents the probable construction of the cell at this stage. We have therefore before us an instance of free cell-formation. The next stage is somewhat difficult to obtain. A change has taken place in the staining capacity of the young spore. As is seen in Fig. 40, the young spore stains more deeply than the surrounding cytoplasm, having evidently absorbed unto itself those materials, cytoplasmic and reserve, which are necessary for its construction. It is not possible now to see the nucleus. In a still later stage the staining capacity of the young spore is still greater, as evidenced by its deeper colour, and by careful observation and the proper amount of staining, the coats of the spore become marked off at the periphery by their denser colour (Fig. 41). In the fourth stage we see a change in the staining capacity of the spore, for the spore-coats being now dense, they prevent the access of the stain. This results, therefore, in the spore again becoming less deeply stained than the surrounding cytoplasm, and it gradually assumes the strongly refractive appearance characteristic of mature spores, giving each spore the appearance of a bright oval speck of light. To examine this stage a more concentrated solution of the stain must be used than the one given above, in order that the walls of the spore may be stained. This stage is seen in Fig. 42. The cytoplasm outside the spore stains only very slightly at this stage, because doubtless most of it has been absorbed by the young spore. This stage is best observed in a three days old culture. In such a culture it is usual to see actively motile individuals in which mature spores are enclosed. The cytoplasm, therefore, cannot all have been absorbed into the spore in such cases, for there must be some left to maintain communication with the cilia, and it is obvious that when all the cytoplasm has been absorbed into the spore, the cilia must drop off and motion cease. This fifth stage is represented in Fig. 43, which shows a mature spore resting inside a perfectly empty sac. Nothing remains except the bare cell-wall. How long the cell-wall can remain intact without disruption must depend on the medium, and more especially on the excreted products. If the latter were acid in reaction, the cell-wall would soon be dissolved. Whatever the dissolving

agent or agents may be, their effect is seen in a slightly older culture where free spores vastly preponderate. Fig. 44 thus represents the final stage. In the last two stages a differentiation of the spore-coat into exine and intine can be observed. This differentiation is first observed in Fig. 42, but the markings of the exine cannot be ascertained till examined either at the Fig. 43 or the Fig. 44 stage.

This description agrees with that given by Meyer for the development of the spore in *Bac. Asterosporus* (9), and by myself for the development of the spore in the genus *Sarcina* (3). There is one point, however, to be observed. Meyer introduces the term 'Sporenvakuole' as indicating the clear space in which the spore is formed, and in my former work I have followed the nomenclature. It seems to me, however, that we are not dealing with a 'vacuole,' but rather with a 'cell,' and this clear space, containing a nucleus and cytoplasm, is of the nature of a cell, and the process is that of free cell-formation, so that the clear space should be referred to as a 'Spore-cell' rather than a 'Spore-vacuole,' for in the ordinary acceptation of the term a 'Vacuole' means a space filled with cell-sap. There are still several gaps connected with the development of the spore which are not yet bridged over. The history of the nucleus which serves as the nucleus of the spore is the most important. Does it migrate into the clear space, being cut off by division from one of the outside nuclei, or is it a nucleus of the cell, around which a clear space has been formed, marking the boundary of the new spore?

This and other problems will not be settled until higher magnifications than we possess at present have been placed at our disposal, or until more ingenious methods of observation have been arrived at.

Motility and Ciliation.

The name *Bacterium hirtum* was given to this form by Henrici (7), because when isolated it was found to be absolutely immotile. In an earlier paper I have shown that any non-motile form can be made motile by continual inoculation, and that *immotile forms of Bacteria* (excluding the thread forms) can be *made motile by the same method* (2). I applied this method to this form (1) and found that it became motile. On making cilia-preparations, the cilia were found to be situated at the poles, and the name of *Bacterium hirtum*, in accordance with Migula's classification, was changed to *Pseudomonas hirtum*. Since then, however (1903), I have kept this form under cultivation for nearly three years and have made a special study of its motility and ciliation. Under continual inoculation the motility once gained has never been lost, but the ciliation is undoubtedly peritrich and not polar, so in accordance with this fact, this form must be allocated to the genus *Bacillus*.

The first indication of motion is seen in a seven hours old culture. As

the material before inoculation was invariably boiled for two minutes at 100° C., every individual was the product of the germination of a spore. The motion exhibited at this stage is of the nature of an undulating and pulling movement. When observed in 2–5-celled individuals (Fig. 11) it is very distinct, more so in fact than in single-celled individuals, probably because they are slightly older, as evidenced by the fact that in them division has occurred once or twice since germination. In longer threads the inertia is too great to produce actual movement, but it is evident that there are cilia even at this stage by the manifest strains that are exerted, which is different from the slight trembling due to molecular movement. I was not successful, however, in obtaining cilia preparations from cultures of this age.

In a fifteen hours old culture the motility is very pronounced, the individuals being as active as any bacillus at its most active stage of motility. Fig. 45 is a micro-photograph and shows two individuals covered with cilia. As seen the cilia are undoubtedly peritrich, so that it is necessary to allocate this species to the genus *Bacillus*. The stain which I employed for cilia preparations was Night-blue, which is made up as follows:—

A. { 1 gram Tannin to 20 c.c. Water.
{ 1 gram Alum to 20 c.c. Water.

B. ½ gram Night-blue to 20 c.c. Absolute Alcohol.

Add A to B, not B to A.

The method of preparation of cilia is as follows:—

A coverslip is washed very clean with alcohol, being finally passed through the flame. A glass slide is washed in the same way. A drop of water is placed on three places on the glass slide. Into one of them the material is inoculated. After passing the inoculating platinum loop through the flame and cooling it, a portion from the inoculated drop is placed into the second drop. In the same way a portion from the second drop is placed into the third drop. In this way the third drop though it contains fewer bacteria is almost clean, with scarcely any stainable matter except bacteria in it, so that clean preparations can be obtained. A portion from the third drop is now smeared over the clean coverslip. Care must be taken that the coverslip is so clean, that when the smearing takes place, the liquid does not roll itself up, but tends to spread out over the surface of the coverslip. The smear is usually performed with a platinum wire. To facilitate the process of smearing about 3 m.m. of the end of the wire is bent at right angles to the rest of the wire, the smearing being performed by this bent end. After the smear dries up, the stain is passed through a filter, allowed to drop on the coverslip and allowed to act for two minutes. The coverslip is then washed, dried, mounted in Xylol and examined.

This method of procedure is simpler and more expeditious than Löffler's method, and in cases where the individuals are actively motile is always to be recommended. This is a good stage for examining the kinds

of motion which are to be observed in this genus. It seems doubtful that the cilia can account for all the different varieties of motion. Recently it has been shown (8) that very probably the motility of the diatoms is due to the evolution of oxygen gas, which sufficiently accounts for the vagaries of these individuals. It is possible that the motion of any particular microbe is the resultant of these two forces, the vital activity of the cilia, and the movement caused by the evolution of gas. It would be interesting to compare the movements of a form of bacteria in which gas is known to be evolved, e.g. *Bacillus coli-communis*, with the movements of a non-gas-producing form, in order to ascertain whether there would be any differences due to the evolution of gas affecting the nature of the motility.

When twenty-four hours old cultures are examined, there is never a lack of active motion in normally developed growths. This age is usually best suited for cilia preparations. In Fig. 46 is shown one made from a culture of this age. In a three days old culture, unless spore-formation is very far advanced, which, as stated above, is not usually the case, the majority of the individuals are still motile. Usually at this stage a small number have either proceeded too far in the formation of spores or else, as is seen in the reduced intensity with which they take up stains, are either dead or in an extremely unhealthy condition. In both these cases there is no motility. In individuals, however, in which no spores are being formed or in which spore-formation is not far advanced, the motility is as great as in younger cultures. In the further growth of the culture the motility ceases owing to the extensive formation of spores, but even in 10–15 days old cultures there can always be seen a few motile individuals. As in reinoculation these asporogenous individuals divide and multiply, it is advisable before reinoculation to heat the material sufficiently to kill these forms but not the spores, if it be desired to obtain an abundance of spores. So far as motility of bacteria in general is concerned, as previously stated I do not think that a single cylindrical or round form of bacteria exists which cannot be made motile by suitable cultivation. In all forms which I have examined persistency in continual inoculation has invariably produced this result, so that motility in bacteria is a question of degree and not a question as to its existence or non-existence. It is important to emphasize this point, because the two latest and best classifications, viz. by Fischer (5) and by Migula (11), adopt the presence or absence of motility as a mark of ordinal importance, whereas, as a matter of fact, it is not even a specific value.

Contents of the Cell.

To secure the material in the most favourable condition, the material must be fixed in a drop of 50% Formol for about three or four minutes. Then the stain (preferably Fuchsin) is added by means of a platinum-loop,

until the requisite intensity is obtained. The exact time and amount can only be decided by repeated trials, and determining, by examination of samples under the microscope, whether the necessary intensity has been obtained. In my own experiments three loopfuls of Fuchsin, prepared as for nuclear staining, allowed to act on the material contained in 50% Formalin for about eight minutes, gave the best results. The cell wall is shown distinctly (Fig. 47) as a uniform deep-red covering to the cell (if Fuchsin be used), whereas the cytoplasm is much more faintly stained. If the proper intensity has been obtained it will be noticed that the cytoplasm is not uniformly stained: patches of much fainter colour appear (Fig. 49). These are not of equal size and are evidently the vacuoles characteristic of mature cells. Throughout my investigation on this form I have not once seen any other differentiation of the cytoplasm, so that it would appear as if all the substances used for metabolic or reserve purposes were stored in the semi-liquid condition inside these vacuoles. I was also not able to distinguish the nucleus. This was rather surprising, inasmuch as I was able to see this structure in *Bac. Asterosporus*, and also in the first stage in the development of the spore. In the latter case, however, it must be remembered that the nucleus is encased by a film of cytoplasm, is attached by strands of cytoplasm to the remainder of the protoplasm of the cell, and is inserted in a faintly staining area, so that it becomes a much more conspicuous object (Fig. 36). The internal structure thus accords with that of the majority of Bacteria, and is in sharp contrast to that of such forms as *Spirillum volutans* (*Spir. giganteum*?), in which the cell is always full of fat-globules and 'volutans-spheres.' The vacuoles are very difficult to observe, but once the proper intensity has been obtained it will be found that they are universally present in all mature cells. I have not been able to demonstrate their presence in newly germinated cells. It is probable that, as in newly formed vegetative cells in other plants, the vacuoles do not appear until the cells reach their maturity. They have the varieties of size and shape characteristic of vacuoles, and their presence accounts for the absence of other indications of the presence of reserve or excreted matters, for these are doubtless to be found inside the vacuoles. The cell wall is seen more distinctly when plasmolysis takes place, for the cytoplasm, owing to the withdrawal of water, contracts, leaving a clear space between the cytoplasm and the cell wall (Fig. 48).

Most Constant Characteristics of Bacillus hirtus.

The following characteristics may be accepted as the most constant.

Spore 1·0–1·8 μ broad, 1·5–2·5 μ long. Slightly oval, differentiated into exine and intine. Exine is bluntly pointed at both ends.

Germination follows by means of an equatorial split. The young

vegetative cell soon protrudes and divides to form a two-celled individual. Immediately after germination one-celled and two-celled individuals are almost exclusively found.

Motility commences very soon after germination and persists till the cytoplasm is removed by the act of forming spores.

On *Nutrient-Agar* after fifteen hours is found a uniform lightish-grey growth, extending either after this period or at furthest after twenty-four hours over the surface of the condensed water. In the healthy condition, when consisting only of one-celled and two-celled individuals, the length varies from 2·5 μ to 4 μ and the breadth is almost uniformly about 1·25 μ (Fig. 21), but later the cells usually become somewhat longer, up to about 8 μ (Fig. 22). The breadth remains the same in all stages of growth. Normally spore-formation commences after three days.

Gelatine plate cultures. Colonies first make their appearance as minute grey specks. Sooner or later the gelatine is liquefied. The colonies, however, often show stratification with a 'nucleus' at the centre, and sometimes exhibit zig-zag outgrowths from the surface.

Agar-plate cultures. Whitish colonies appear on the surface after twenty-four hours, sometimes in less time. The colonies may reach a diameter of 2–2½ m.m. in twenty-four hours, or may have spread over the whole surface of the Agar-plate. Sometimes the Agar gives the appearance as if it were partially liquefied. Occasionally the culture takes on a deep bronze colour. Formation of spores very plentiful.

Gelatine-stab cultures. Growth appears as a light grey fleck on the surface of the gelatine. This grows larger, may or may not cover the whole surface of the gelatine. Gelatine is liquefied. When liquefaction takes place there is present a whitish-grey sediment at the bottom of the liquefied part. The liquid is yellowish-brown in colour and turbid.

Growth in liquid media. Grows in the following liquid nutrient media. (See text.)

O. Strong growth. Thick pellicle on surface. Strong acid reaction. Spore-formation postponed.

I. Strong growth. Thick pellicle on surface. Strong acid reaction. Spore-formation postponed.

III. Slightly weaker growth. Thick pellicle on surface. Gelatinous or mucinous precipitate. Strong alkaline reaction.

VI. Weaker growth. Thin pellicle on surface. Acid reaction.

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EXPLANATION OF PLATE.

Figs. 1–4, 6, 10, 15–20, 23–29, 48–49 drawn with drawing apparatus. Magnification 1650.

Fig. 1. Spore stained with Iodine, showing intine strongly and exine faintly coloured.

Figs. 2–3. Spores stained with Methylene-blue.

Fig. 4. Spore stained with Fuchsin, exine coloured, intine untouched by stain.

Fig. 5. Spore very highly magnified to show exine and intine.

Fig. 6. Spore stained with Methylene-blue seen 'end on.'

Figs. 7–9. Stages in germination of the spore.

Fig. 10. Appearance of individuals in a five hours old culture. Chains of two-celled individuals.

Fig. 11. A two-celled individual. Appearance of individuals when growing under optimum conditions of growth.

Fig. 12. Portion of a filament in which very prolific formation of spores has taken place.

Figs. 13–14. Gelatine stab-cultures. See text for explanation.

Fig. 15. Individuals from Nutrient medium No. 1 culture.

Figs. 16–17. Individuals from Agar culture. Fifteen hours old.

Fig. 18. Cilia preparation from a two days old Agar culture.

Fig. 19. Spore containing individual stained with Fuchsin, in which abundant cytoplasm is found in the vegetative cell, even after the spore is completely ripe.

Fig. 20. Cilia-preparation from a four days old Agar culture.

Fig. 21. Schematic representation of length of individuals from a twenty-four hours old Agar culture. The transverse line indicates cell-division at that point.

Fig. 22. Same from a two days old culture.

Fig. 23. Two-celled individual in which a division wall is formed, before elongation has taken place.

Fig. 24. Two-celled individual in which a division wall is formed after very slight elongation.

Figs. 25–34. Stages in cell-division. For explanation see text.

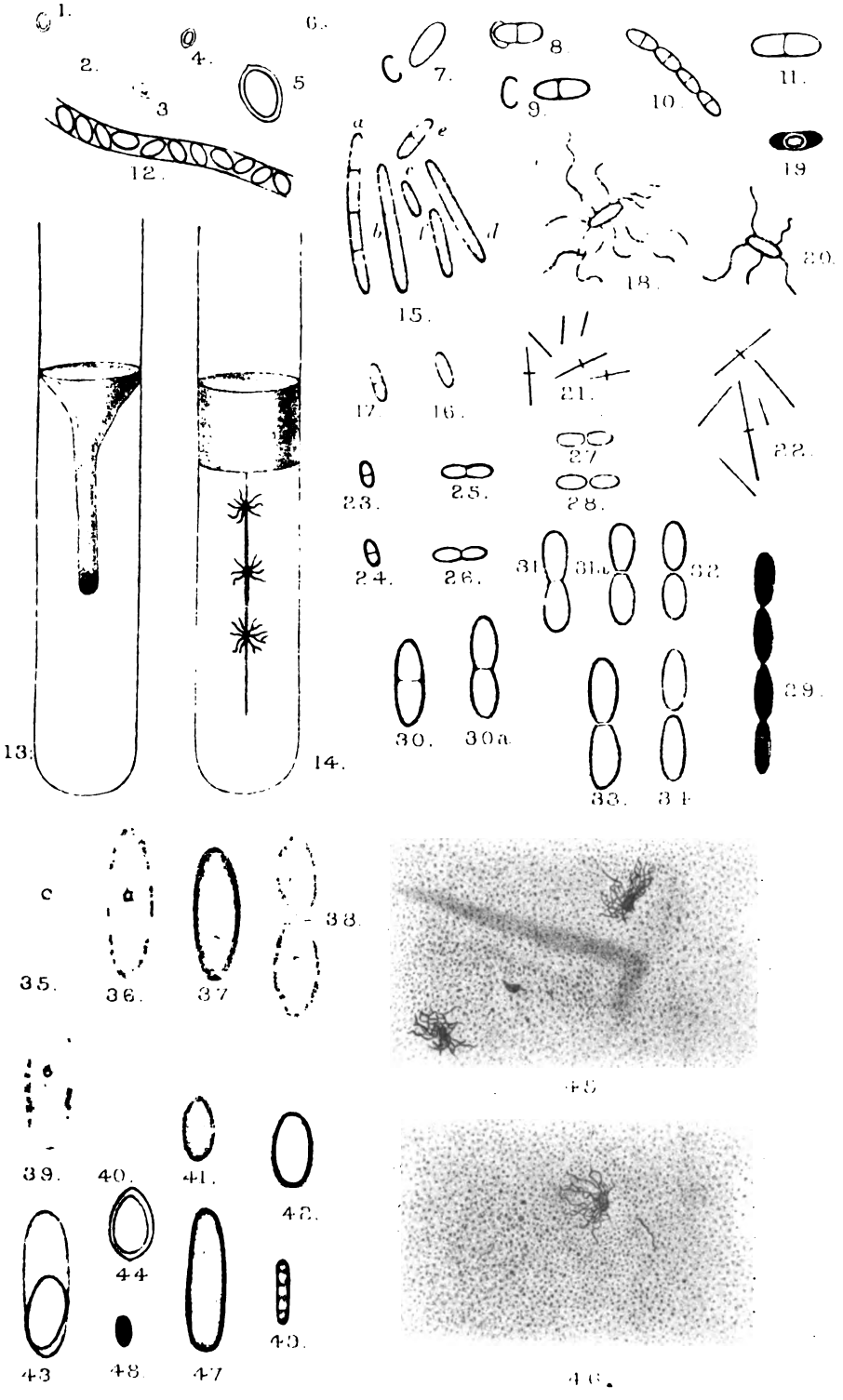
Figs. 35–44. Stages in spore development. For explanation see text.

Figs. 45–46. Micro-photographs taken with 1/12 oil-immersion lens to show distribution of cilia. Cilia stained with Night-blue. Kindly photographed by Mr. Garry.

Fig. 47. Cell stained with Fuchsin to show cellular membrane.

Fig. 48. Plasmolysed cell which separates the cell-wall from the protoplasm.

Fig. 49. Cell stained with Fuchsin to show cellular membrane.



ELLIS — BACILLUS HIRTUS.

Some Points in the Morphology of Phyllocladus alpinus, Hook.

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With Plates XVII and XVIII.

I. Introduction.

PHYLLOCLADUS is a peculiar and isolated genus belonging to the Taxaceae, and characterized by the reduction of its true leaves to pointed scales, and the expansion of certain of its stem-branches into flattened leaf-like structures. Pilger in his monograph of the Taxaceae [1] places the genus in a sub-family by itself, intermediate between Podocarpoideae and Taxoideae. There are six species confined to New Zealand, Tasmania, and the Indian Archipelago. The isolated systematic position of the genus, its restricted distribution and curious external morphology, added to the fact that little was known of its anatomy or development, suggested to Prof. F. W. Oliver that it might prove an interesting subject for investigation. Accordingly, through the kindness of Dr. L. Cockayne, who had access to *Phyllocladus alpinus*, the Celery Pine of New Zealand in cultivation in the Christchurch Botanic Garden, five gatherings of material were sent to University College during the years 1902, 1903, and 1904, and were handed to me for examination. The following account is based upon this material, supplemented by a supply of the vegetative organs of two other species, *P. rhomboidalis* and *P. trichomanoides*, which Mr. R. I. Lynch, M.A., was so kind as to obtain for me from the Edinburgh Botanic Garden, and which has been very useful for comparison. The material of *P. alpinus*, which was fixed in methylated spirit, was unfortunately inadequate for anything like a complete investigation, and it is greatly to be desired that some one who has access to the genus in its native haunts should give us an exhaustive account of its morphology. I am much indebted to Prof. Oliver for his kind help and advice throughout the work.

[1] R. Pilger, Das Pflanzenreich, iv, 5, Taxaceae, 1903.

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II. The Vegetative Organs.

The first extant figure of *Phyllocladus* was published exactly eighty years ago by L. C. Richard [1]; it is an exquisite engraving of *P. rhomboidalis*, the only species then known. The main peculiarity of the vegetative structure, to which I have already referred, is the reduction of the leaves to more or less ephemeral scales, and the development of lateral stem-branches into cladodes (Fig. 1). The cladodes arise in the axils of leaves, and consist not merely of a single flattened lateral axis, but in many cases of a whole system of branches fused edge to edge. In fact, in the words of Bertrand [2], 'le cladode de *Phyllocladus* n'est pas, en général, un rameau unique, aplati en forme d'expansion foliacée, c'est tout un système de rameaux tertiaires et secondaires soudés entre eux et au rameau primaire sur lequel ils sont nés.' The veining of the larger limb of the cladode in Fig. 1 shows the complex nature of the organ; the secondary leaf-traces are easily distinguished from the vascular systems of the tertiary lateral shoots occurring in their axils. The leaves are best studied in sections of the apical leaf-buds, since they soon fall off and are represented only by scars (cf. Fig. 6 and Fig. 1). The leaves are very simple structures, triangular in section, traversed by a single small collateral bundle accompanied by a resin passage. There is no differentiation into spongy and palisade parenchyma, and in our species I have not observed any stomates. Stomates appear also to be absent in the leaves of *P. trichomanoides*, but in *P. rhomboidalis* I have observed a few. In transverse sections of the main axis each leaf-trace is seen to leave the ring of vascular strands accompanied internally by two much larger bundles destined to supply the axillary branch [3] (Fig. 7). If the branch is followed upwards it is found to remain for some little distance fused with the main axis, but the two bundles divide to form a small complete ring, so that a transverse section may show the main vascular rings and one or more subordinate vascular rings side by side with it. If the axillary branch is destined to form a cladode instead of a cylindrical axis it becomes much flattened, and the arrangement of the bundles resembles (in a simple case) that shown in Fig. 2, or some variant on it. The assimilating tissue of the cladode shows a slight differentiation, but this is much more marked in *P. trichomanoides*, where there is a fairly distinct development of palisade parenchyma on one side. The epidermis is strongly cuticularized, and the stomates, which in the three species examined are not confined to one face of the cladode, are well protected (Fig. 5). In the cortex of

[1] L. C. Richard, Commentatio Botanica de Conifereis et Cycadeis, 1826.

[2] C. E. Bertrand, Anatomie comparée des tiges et des feuilles chez les Gnétacées et les Conifères. Ann. des Sci. Nat., v^e^ sér., Bot., t. xx, 1874.

[3] Observed by Th. Geyler, Einige Bemerkungen über *Phyllocladus*, Abhand. der Senckenberg, Naturf. Gesellsch., Bd. xii, 1880.

both cladode and normal axis there are a number of large lignified pitted elements.

The most interesting point in the anatomy of the cladode is the occurrence in the lateral bundles of *centripetal xylem*. This is remarkably well developed in *P. alpinus*, and also occurs, though less prominently, in *P. rhomboidalis* and *P. trichomanoides*. The centripetal xylem is not found at the base of the cladode, but only appears higher up. It is confined to the cladode, not occurring in the leaf (Fig. 6), the normal more or less cylindrical main axis (Fig. 7), or the axis of the male or female cone (Figs. 10 and 28). It consists of large tracheids which occur on the inner side of the protoxylem and also flank the normal xylem. These tracheids show the sculpturing which one is accustomed to associate with Taxinean wood,—the combination, namely, of scalariform or spiral thickening with bordered pits. The elements of the normal xylem are also marked in this way, though to a less conspicuous extent. Figs. 3 and 4 show radial and transverse sections of a lateral cladode bundle with well developed centripetal xylem. Taxinean sculpturings are not confined to the wood of the cladode, but occur also in that of the leaf, the young part of the main axis, and the axes of the male and female cones. (I have not had an opportunity of examining an old axis.) We will consider the possible significance of these facts later on.

III. The Reproductive Organs.

A. *The female cone.*

The female cone consists of a branch arising in the axil of a scale leaf and bearing a number of succulent bracts in the axil of each of which grows a single erect ovule. The bracts are as a rule, but not always, decussate. The best-developed cones which I examined had two pairs of fertile bracts at the base, succeeded by several sterile ones which had fused with the cone axis into an irregular terminal mass. Often two or three cones are closely clustered together, in which case the number of bracts and ovules in each individual cone is apt to be reduced to two. The stalk of the cone contains a ring of normal collateral bundles (Fig. 10). The appearance and structure of the cone and ovule shortly after pollination (which appears to occur in October) will be understood from Fig. 1 and Figs. 8–16. The nucellus contains the endosperm, surrounded by a well marked megaspore membrane, and is free right down to the base (Fig. 11). It is surrounded by a thick integument which is strengthened by a fibrous layer a little below the surface. After pollination the closure of the micropyle is effected by the growth and tangential division of the epidermal cells (Figs. 12, 13, A and B). The arillus at this stage is a mere ring-like upgrowth round the base of the ovule. No vascular strands enter the integument; they terminate in a tracheal platform below the base of the nucellus.

Fig. 17, A and B, shows an older cone and seed, while Fig. 18 represents a radial section of the base of such a seed. The arillus is now a conspicuous papery cup. The walls of the fibrous layer have increased to an enormous thickness, and each cell contains a conspicuous crystal (Fig. 21, A and B). The elements composing the tracheal platform have very characteristic Taxinean sculpturing (Fig. 20). Between the tracheal platform and the megaspore is a palisade of long cells with bordered pits (Fig. 19). Unfortunately the preservation of the female cones was too poor and the stages were too few to allow the events within the embryo sac to be followed. Sections of the nucellus of cones gathered two or three months after pollination, such as those shown in Fig. 22, often reveal a small pear-shaped embryo deeply embedded in the endosperm (Fig. 23). The megaspore-membrane at this stage is remarkably clear (Fig. 24).

B. *The male cone.*

The material sent by Dr. Cockayne included three or four male cones gathered just as they were shedding their pollen (Fig. 26). Each sporophyll bears two pollen-sacs on its underside. Sections of a cone which had not dehisced revealed the fact that the ripe pollen-grain was of the Podocarpoid type[1],—winged and containing four nuclei (Fig. 27). Curiously enough, two of the cones sent showed abnormalities. One was hermaphrodite, bearing an ovule at the base succeeded by stamens (Fig. 25), while in a second the axis, instead of being simple, was branched at a point two-thirds from its base.

IV. The Affinities of *Phyllocladus*.

Strasburger (Die Coniferen und die Gnetaceen, 1872) places *Phyllocladus* in the subdivision Podocarpeae of the Taxaceae, but regards it as coming nearer to the Taxeae (Taxus, Torreya, Cephalotaxus, and Ginkgo) than do the other members of the same subdivision. Pilger (Taxaceae, 1903) consigns *Phyllocladus* to the separate group Phyllocladoideae, intermediate between Podocarpoideae and Taxoideae. The difference between these two positions is not a radical one, but my observations make me feel that the earlier view is perhaps the more expressive. The affinity with the Podocarps is undoubtedly the stronger, though there are distinct indications of a Taxoidean relationship as well.

The main points in which *Phyllocladus* resembles the Podocarpoideae and differs from the Taxoideae are as follows :—

1. *Each carpel bears a single ovule.* In the Taxoideae each carpel is bi-ovulate.

[1] W. C. Coker, The Gametophytes and Embryo of Podocarpus. Bot. Gaz., vol. xxxiii, 1902, p. 89.

2. *The stamens bear two pollen-sacs only.* In the Taxoideae there are more than two pollen-sacs.

3. *The ripe pollen-grains are winged and contain four nuclei.* In the Taxoideae the pollen-grains have one or two nuclei and no wings.

4. *There is a well-marked megaspore-membrane.* In the Taxoideae the megaspore membrane is *never* well-developed, whereas in the Podocarpoideae it is present and well-marked in *Dacrydium*, though absent in *Podocarpus*[1].

The points in which *Phyllocladus* approaches the Taxoideae and differs from the Podocarpoideae are as follows:—

1. *The ovule is erect.* This is a decidedly important point. The ovule of the Podocarps is characteristically inverted, but in certain instances it is erect or nearly so, e.g. *Dacrydium latifolium.*

2. *A symmetrical arillus is present.* The arillus of *Phyllocladus* recalls that of *Taxus* except that it is not succulent. The ovules of the Podocarpoideae, on the other hand, have an 'epimatium' which resembles an arillus, but is characteristically one-sided instead of symmetrical, and is regarded by Pilger (l. c.) as an outgrowth from the carpel, and not homologous with the arillus of the Taxoideae. We must remember, however, that the asymmetry of the epimatium is correlated with the inverted position of the ovule, so that it will not do to lay too much stress on this point, as proving that epimatium and arillus are not homologous.

3. *Centripetal wood occurs in the cladodes.* It is difficult to say what importance, if any, should be attached to the presence of centripetal wood in so specialized an organ as a cladode. May we regard it as suggesting Taxoidean affinity? The Taxoideae show more indications of centripetal wood than the other Coniferae[2]. It has been observed in the leaf and cotyledon of *Cephalotaxus*[2] and *Taxus*[2], and in the cotyledon of *Torreya*[3], and in the stem of *Cephalotaxus koraiana*[4]. The last case is of importance as it is the only instance so far known among recent Coniferae of centripetal xylem in an axial organ. *Cephalotaxus koraiana* is sometimes regarded as merely a fastigiate variety of *C. drupacea*, or *C. pedunculata*, but Rothert is inclined to regard it as a distinct species. It is difficult to determine how much stress to lay on the case of the appearance of centripetal xylem in a single species of a genus, while closely allied species, or it may be even varieties of the same species, are quite normal. But I think its appearance, taken in connexion with the other cases known

[1] R. B. Thomson, The Megaspore Membrane of the Gymnosperms. Univ. of Toronto Biol. Series, No. 4, 1905.

[2] W. C. Worsdell, On 'Transfusion-tissue': its Origin and Function in the Leaves of Gymnospermous Plants. Trans. Linn. Soc., vol. v, 1897.

[3] Edith Chick, The Seedling of Torreya myristica. New Phyt., vol. iii, 1903, p. 83.

[4] W. Rothert, Ueber parenchymatische Tracheïden und Harzgänge im Mark von *Cephalotaxus-Arten.* Ber. d. Deutsch. Bot. Gesellsch., Bd. xvii, 1899, p. 275.

in the family, at least strengthens the presumption that a tendency to the production of centripetal xylem is a hereditary character of the Taxoideae. So I am inclined to believe that the occurrence of centripetal xylem in the cladodes of *Phyllocladus* is quite possibly due to an inherited tendency derived by both *Phyllocladus* and the Taxoideae from some common ancestor, and apt to reappear when a special combination of circumstances renders it appropriate. In the case of *Phyllocladus* the use of the centripetal xylem is not far to seek. As shown in Fig. 2 the cladode is flattened parallel to a plane which would symmetrically divide the lateral bundles, i. e. the latter occupy a position at right angles to that which they would take up if the cladode was a leaf. An extension of the xylem in the plane of flattening of the organ is brought about in leaves by wings of transfusion tissue *lateral* to the bundle (e. g. *Podocarpus*), whereas in *Phyllocladus* an extension of the wood in a corresponding plane necessarily brings centripetal xylem into existence. If we suppose that the centripetal xylem is an ancestral character, one alternative is to imagine that at that remote period when the cladodes were first being evolved the axis and leaves still possessed internal xylem, so that the cladode naturally possessed it as well; it must then have gradually disappeared from the axis and leaves, while it was retained in the cladode owing to its usefulness. On the other hand, it is, I think, open to us to suppose that the internal xylem was completely lost in stem and leaves before the flattened leaf-like branches were ever developed, but that when the cladode was evolved the need of lateral transmission of water awoke, as it were, a forgotten memory, and the plant once again took up the formation of centripetal xylem.

4. *Taxinean sculpturing occurs in the tracheids.* In *Phyllocladus alpinus* tracheids with the characteristic Taxinean markings (a combination of bordered pits and spiral or scalariform thickenings) occur in the xylem. Tracheids of this kind, though by no means confined to the Taxoideae, are sufficiently characteristic of it to make their appearance in *Phyllocladus* distinctly suggestive of affinity.

V. Summary.

The main result of this investigation is to confirm the view of the systematists that *Phyllocladus* occupies an intermediate position between Podocarpoideae and Taxoideae, but with greater affinity for the former. The existence of winged multi-nucleate pollen-grains ratifies the Podocarpoid affinity, while the presence of centripetal xylem in the cladode is regarded as a 'harking-back' to a hypothetical common ancestor of Taxoideae and Phyllocladoideae which possessed bundles of this type.

EXPLANATION OF PLATES XVII AND XVIII.

Illustrating Miss A. Robertson's paper on *Phyllocladus alpinus*.

r. = resin passage; *x.* = normal xylem; *cpx.* = centripetal xylem; *ph.* = phloem; *st.* = stomate; *px.* = protoxylem; *b.* = paired bundles going to a branch; *l.t.* = leaf-trace; *l.b.* = leaf base; *sc.* = scar of attachment to cone axis; *ar.* = arillus; *br.* = bract; *o.* = ovule; *pr.* = prothallus; *m m.* = megaspore membrane; *p.t.* = pollen-tube; *n.* = nucellus; *i.* = integument; *scl.* = sclerized layer of integument; *p.p.* = platform of pitted cells; *p.tr.* = tracheal platform; *emb.* = embryo; *s.* = suspensor; *i.* = idioblast.

PLATE XVII.

Fig. 1. Branch showing ♀ cone shortly after pollination, cladode, leaf-bud, and leaf-scars. × 4 *circa.*

Fig. 2. Diagrammatic transverse section of cladode. × 28.

Fig. 3. Rather young lateral bundle cut radially, from tangential section of a cladode. × 386.

Fig. 4. Transverse section of lateral bundle from a cladode. × 386.

Fig. 5. Stomates from transverse section of a cladode. × 386.

Fig. 6. Transverse section of terminal leaf-bud such as that shown in Fig. 1. × 74.

Fig. 7. Diagrammatic transverse section of an axis. × 28.

Fig. 8. Cone (same age as Fig. 1) cut lengthways. × 3 *circa.*

Fig. 9. Ovule and bract (same age as Fig. 1). × 3 *circa.*

Fig. 10. Diagrammatic transverse section of cone-stalk drawn in Fig. 1. × 28.

Fig. 11. Radial section of ovule and bract shortly after pollination. × 28.

Fig. 12. Transverse section at A, Fig. 11. × 28 and × 74.

Fig. 13. Transverse section at B, Fig. 11, showing closure of micropyle. × 28 and × 74.

Fig. 14. Transverse section at C, Fig. 11. × 28 and × 74.

Fig. 15. Longitudinal section at D, Fig. 11. × 74.

Fig. 16. Longitudinal section at E, Fig. 11. × 74.

Fig. 17 (A and B). Cone and seed somewhat older than that shown in Fig. 1. × 4 *circa.*

Fig. 18. Longitudinal section of base of seed shown in Fig. 17 B. × 28.

Fig. 19. Single pitted cell from palisade below megaspore. See *p.p.* in Fig. 18. × 386.

Fig. 20. Short tracheids from platform at base of seed. See *p.tr.* in Fig. 18. × 386.

Fig. 21. Details of sclerized layer in integument of seed whose base is shown in Fig. 18; A, nearer base; and B, higher up. × 386.

PLATE XVIII.

Fig. 22 (A and B). Two views of cone two or three months older than that shown in Fig. 1. × 5 *circa.*

Fig. 23. Endosperm of cone of age of Fig. 22 showing embryo and suspensor. × 43.

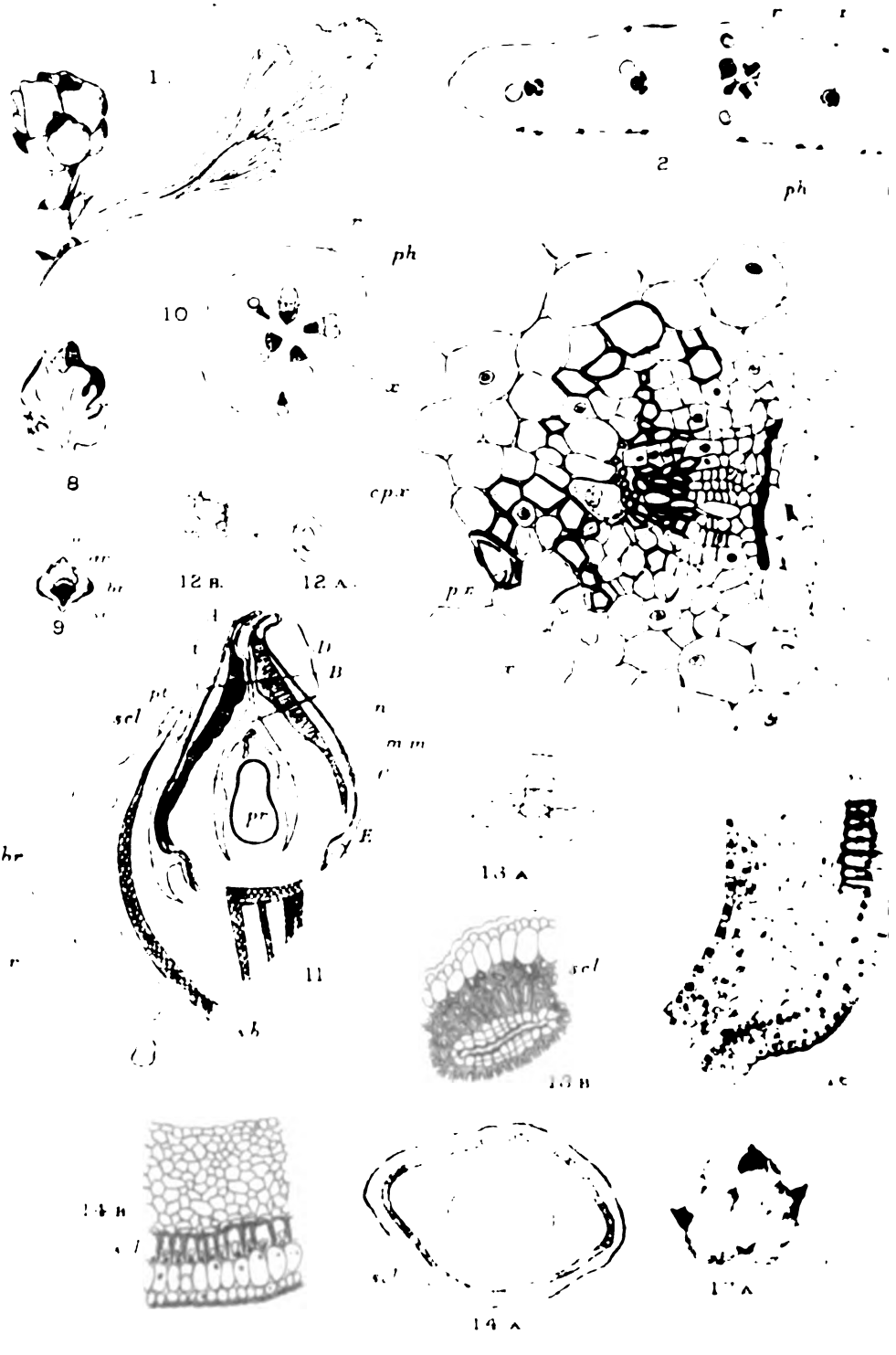
Fig. 24. Edge of endosperm showing megaspore membrane. × 580.

Fig. 25. Hermaphrodite cone. × 7 or 8.

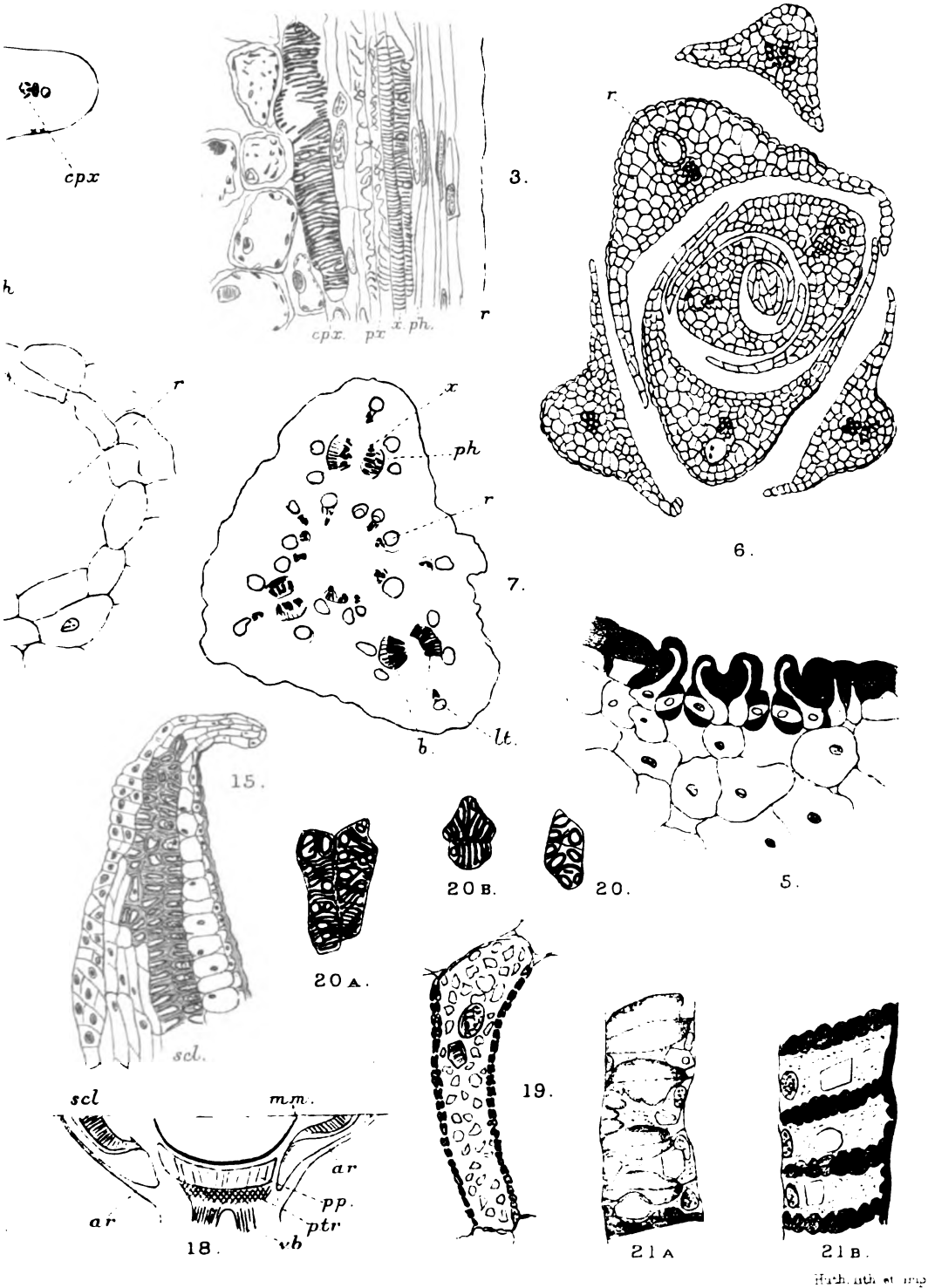
Fig. 26. Normal ♂ cone. × 7 or 8.

Fig. 27. Ripe pollen-grain. × 580.

Fig. 28. Transverse section axis of ♂ cone below stamens. × 112.



ROBERTSON — PHYLLOCLADUS ALPINUS



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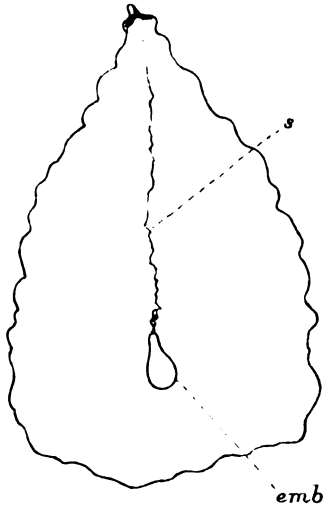
22 A.

22 B.



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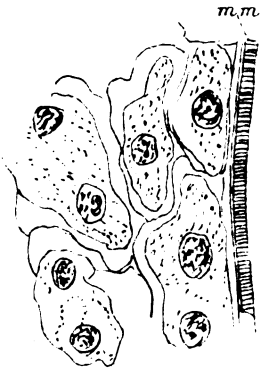

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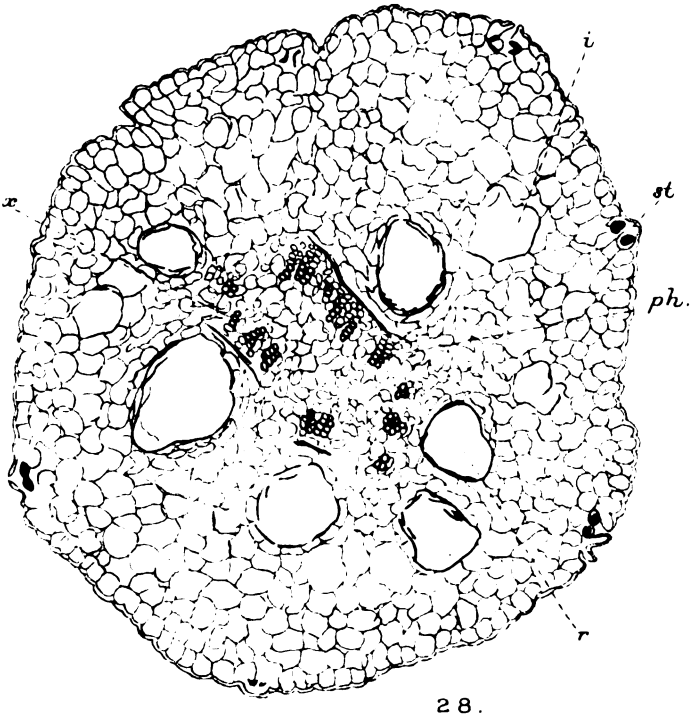

28.

A R del.

Huth, lith et imp.

ROBERTSON — PHYLLOCLADUS ALPINUS.

On the Presence of a Parichnos in Recent Plants.

BY

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With Plates XIX and XX.

THE term Parichnos was used by Bertrand [1] to designate the thin-walled parenchymatous strand of tissue, occurring in *Lepidodendron Harcourtii*, which accompanies the leaf-trace on the posterior side during its outward journey. It is described as originating in the middle cortex, and during its passage through the suberized zone—i. e. the outer cortex—the strand bifurcates, the two branches diverge, and eventually occupy a position one on each side of the foliar bundle, forming the well-known lateral prints on the leaf-scar, as seen on casts.

These facts were corroborated by Hovelacque [2] for *Lepidodendron Selaginoides* and by Williamson [3].

Essentially the same features occur in *Syringodendron*. Renault [4] has described the presence of two large lacunae, which accompanied the leaf-trace one on each side in *Sigillaria spinulosa*. He subsequently showed that these spaces were originally filled with a delicate tissue, traversed by secretory canals, and that each parichnos-strand was surrounded by a sheath of radially elongated elements.

Maslen [5], in his work on *Lepidostrobus oldhamius*, found that the parichnos was represented by an empty space of considerable size; there was no indication of branching, and, as regards this last point, he remarks that, 'this difference may perhaps be correlated with the small width of the proximal end of the pedicel, as compared with that of the leaf-base in the vegetative region.'

[1] Bertrand, Remarques sur le Lepidodendron Harcourtii de Witham. Travaux et Mémoires des Facultés de Lille. T. ii, 1891.

[2] Hovelacque, Recherches sur le Lepidodendron Selaginoides, Sternb. Mem. Soc. Linn. Normandie, xvii, 1892.

[3] Williamson, Organization of the Fossil Plants of the Coal Measures, part xix, Phil. Trans. Roy. Soc. Lond. B., 1893.

[4] Renault, Flore fossile d'Autun et d'Épinac.

[5] Maslen, The structure of Lepidostrobus. Trans. Linn. Soc. Lond., 2nd ser., Bot., vol. v, 1899.

[Annals of Botany, Vol. XX. No. LXXIX July, 1906.]

Scott[1] has called attention to the occurrence in the mature seed of *Lepidocarpon Lomaxi* of two gaps, one on either side of the bundle, which are strongly suggestive of a parichnos, and mentions that a really sharp differentiation of this tissue is only found near the base of the sporophyll. Further, when dealing with the structure of the axis of the strobilus, he remarks the presence in the sporophyll of a strand of large-celled tissue, which probably represents the parichnos of the vegetative leaf base of the Lepidodendreae.

Weiss[2] describes in *Lepidophloios fuliginosus*, a group of cells which, in connexion with each foliar bundle, passes through the outer cortex to the leaves where they form the so-called parichnos.

Thus it is obvious that the parichnos was a tissue of wide occurrence in the fossil forms of the Lycopodineae, and that it occurred both in the sporophyll and foliage leaf.

From a survey of the literature, still more so from the examination of the published figures, and from the actual preparations, one feature stands out with remarkable clearness, which is, that the different plants and specimens exhibit the parichnos preserved in very diverse conditions. At one extreme the tissue is represented by canals, as in the mature seeds and sporophylls of *Lepidocarpon* and *Lepidostrobus*; at the other extreme there is a very definite parenchymatous strand as described by Williamson, Bertrand, Hovelacque, Seward[3] and A. W. Hill[4], and others. In an intermediate position there are specimens showing the tissue in different stages of disintegration.

This feature is capable of a simple explanation, which is, that these seeming discrepancies are due, in many cases, to the fact that the parichnos has been preserved in different stages of development: the empty canal being the mature structure.

Whether this be true for all cases, palaeophytologists will be able to judge far better than the writer.

Turning to what has been termed[5] parichnos in recent plants, it may be seen best in *Isoetes Hystrix*.

The mature sporophyll of this plant exhibits two canals (Fig. 1) running longitudinally, and situated, one on each side of the sporogenous mass, in

[1] Scott, D. H. The seed-like fructification of Lepidocarpon, a genus of Lycopodiadaceous cones from the Carboniferous formation. Phil. Trans. Roy. Soc. Lond., vol. cxciv, 1901.

[2] Weiss, A biseriate Halonial branch of Lepidophloios fuliginosus. Trans. Linn. Soc. Lond., 2nd ser., Bot., vi, 1903.

[3] Seward, Notes on the Binney Collection of Coal-Measure plants, part i: Lepidophloios. Proc. Phil. Soc. Cambridge, x, 1899.

[4] Seward and A. W. Hill, On the structure and affinities of a Lepidodendroid stem from the calciferous sandstone of Dalmeny (Scotland), probably identical with Lepidophloios Harcourtii, Witham. Trans. Roy. Soc. Edin., xxxix, 1900.

[5] Hill, T. G., On the presence of Parichnos in Recent Plants. Brit. Assoc., Sect. K., Cambridge, 1904.

the lateral expansions of its base. The passages when mature (Fig. 4) contain mucilage, and, unlike the parichnos of fossil plants, they do not extend into the cortex of the stem, but are entirely confined to the base of the sporophyll, their limits seemingly depending on the extension of the sporangium.

Their development follows the normal course for lysigenous mucilaginous degeneration.

The first appearance is indicated by the swelling of the walls of the parenchyma, and the gradual disappearance of the cell-contents. This is shown by the marked density of the staining, as compared with the surrounding tissue (Fig. 2). The process of degeneration goes on rapidly, and lacunae appear, so that there is formed a central cavity (Figs. 3, 4, 15 and 17). This cavity gradually extends radially, ultimately resulting in an extremely well-marked mucilage-canal more or less circular in outline.

As regards the sterile leaves, *Isoetes Hystrix* does not form many, and, apparently, they do not possess the parichnos-strands.

Unfortunately it has not been possible to examine satisfactory material of any other species of *Isoetes* with the exception of *I. lacustris*, which plant does not show any sign of the structure in question.

Other living representatives of the Lycopodineae have naturally been examined.

In the case of *Lycopodium*, Hegelmaier[1] showed that the leaves of *L. inundatum* and *L. alopecuroides* are traversed throughout their whole length by a mucilage-canal, which enters the cortex of the axis where it ends blindly. In the young leaves, these canals are represented by thin strands of parenchymatous tissue somewhat merismatic in appearance. De Bary[2] draws attention to similar passages occurring in the marginal expansions, on the dorsally winged sporophylls, of *L. annotinum*.

Jones[3] corroborates Hegelmaier regarding the presence of the mucilage-canals in *L. inundatum*, and states that these structures were not observed in the vegetative leaves in the other species examined, viz. *L. alpinum*, L., *L. annotinum*, L., *L. cernuum*, L., *L. Chamaecyparissus*, A. Br., *L. clavatum*, L., *L. complanatum*, L., *L. Dalhousieanum*, Spring., *L. nummularifolia*, Blume., *L. obscurum*, L., *L. Phlegmaria*, L., *L. Selago*, L., *L. serratum*, Thunb., and *L. squarrosum*, Frost.

Many of these species have been examined by the writer, who corroborates the observations made by Jones regarding this point, with the exception of the case of *L. cernuum*. Although the mucilage-canals are frequently absent from the vegetative leaves, they are often present in the

[1] Hegelmaier, Zur Morphologie der Gattung Lycopodium. Bot. Ztg., 1872.

[2] De Bary, Comparative anatomy of the Phanerogams and Ferns. Oxford, 1884.

[3] Jones, The morphology and anatomy of the stem of the genus Lycopodium. Trans. Linn. Soc. Lond., 2nd ser., Bot., vii.

sporophylls. Thus it has been found that the following plants have more or less extensive mucilage-cavities in the strobili, but not in the ordinary vegetative parts:—*L. alpinum*, *L. annotinum*, *L. caroliniatum* and *L. clavatum*. On the other hand these passages have not been seen in any part, vegetative or reproductive, of *L. Phlegmaria*, *L. squarrosum*, and *L. complanatum*. *L. cernuum* has the structure particularly well marked both in the cone and vegetative regions (Figs. 12 and 13).

Taking for an example *L. clavatum*, it has been found that the development follows an essentially similar course to that already described for *I. Hystrix*, hence no detailed description is requisite.

A series of transverse sections through a young sporophyll (Figs. 5, 6, 7 and 8) demonstrate, that in the more distal regions the young parichnos consists of two rather ill-defined strands, which in passing towards the axis rapidly merge one into the other, so that when the stem is reached a broad zone of disorganizing tissue is produced. The examination of longitudinal sections shows that this lysigenous degeneration extends from the sporophyll into the cortical region of the stem downwards, almost as far as the insertion of the next leaf (Figs. 9, 10 and 11). When the canal is fully formed, the parichnos forms a single continuous structure, and it shows no signs of bifurcation; indeed, it is only in the youngest stages of development that a double origin can be made out, and then only at its distal limits in the sporophyll. Thus a difference is exhibited between this plant and *Isoetes*, but it is to be borne in mind that the same dissimilarity occurs in different fossil plants; for example, *Lepidostrobus* has a parichnos consisting of a single cavity, while *Lepidocarpon* possesses the more usual double arrangement.

A certain amount of variation is to be found in the strobili of different species of *Lycopodium*, more especially as regards the extent of the tissue-alteration. This, however, is a minor point of no consequence, and seemingly depends on the shape and other morphological features of the sporophylls.

The vegetative leaf of *L. cernuum* has a prominent canal, and contrary to what obtains in the sporophyll, where the cavity never, in any of the species examined, extends much beyond the region of the sporangium, it traverses the greater part of the leaf, and comes to an end in the cortex of the axis.

Owing to the lack of suitable material, the development of the parichnos of the vegetative regions has not been worked out: there is, however, no reason to suppose that it follows a course in its formation other than the normal.

As regards other genera of the Lycopodineae, many species of *Selaginella* have been examined, but in no case has anything approaching a parichnos been detected, nor has any reference to the existence of mucilage-ducts been found in the literature dealing with the structure of this genus.

This is a result which might have been expected on account of the relative smallness of the leaves. *Phylloglossum* also has given negative results.

The reasons for considering these canals as representing essentially the same structure as the parichnos of fossil plants are sufficiently obvious, and may be briefly enumerated :—

1. Both in recent and fossil plants they occupy the same relative position. On the one hand there is a double strand with the vascular bundle between and slightly above, as in *Lepidophloios* (Fig. 14) and *Isoetes* (Fig. 15); on the other, a single strand beneath the vascular bundle, as in the case of *Lepidostrobus* and *Lycopodium* (Figs. 12 and 13).

2. The appearance in section is frequently identical. The hollow canals of *Lepidocarpon*, for instance, may be compared with the mature structure in *Isoetes*. The parenchymatous strand in *Lepidodendron* is similar to some of the early stages in the development of the canals in *Isoetes* and *Lycopodium*. Thus Figs. 16 and 18, representing the parichnos of *Lepidophloios* and *Lepidodendron* respectively, may be compared with Figs. 15 and 17, illustrating a stage in the development of the mucilage-duct in *Isoetes Hystrix*.

The main point of dissimilarity lies in the fact that in *Isoetes* the parichnos does not extend into the cortex.

This may be considered an unimportant matter—that so ancient a feature should be altered somewhat in recent plants is to be expected, the surprising thing would be to find the tissue entirely identical both in recent and fossil plants.

Function.

It is manifestly a matter of no inconsiderable difficulty to assign a definite function to a tissue of so specialized a nature as the parichnos occurring in fossil plants. Consequently, it is not surprising to find that in this respect the authorities differ. Hovelacque considered the tissue as being glandular, with which view both Williamson and Bertrand disagreed. Renault regarded the tissue as representing gum-canals, Potonié as transpiratory organs. Scott [1], while admitting the possibility of the secretory function, points out that 'the persistence and enlargement of the parichnos on the surface of old stems suggests a respiratory function like that of lenticels.' This view is also held by Weiss [2], who suggests that the parichnos was probably 'a respiratory organ, allowing a passage of air from the leaves into the inner portion of the stem and down into the roots.' He compares the structure with 'the trabecular tissue of various species of *Selaginella*, which also accompanies the leaf traces, and probably has the same function as the middle cortex and the parichnos, but the persistence of the parichnos on the leaf scars of the old stems of *Lepidodendra* enabled

[1] Scott, Studies in Fossil Botany, London, 1900.

[2] Loc. cit.

them also to supply the place of the lenticels of the recent dicotyledonous trees.'

As regards the parichnos of recent plants, I believe that it is primarily concerned in the production of mucilage, which would be of value to the reproductive organs in preventing their desiccation in times of comparative drought. And it is primarily for this reason that the structure has persisted.

The fact that the parichnos is chiefly restricted to the sporophylls of recent plants, as far as has been seen, bears out this opinion. If this view be accepted, it would explain why, in a plant like *Isoetes lacustris*, the parichnos does not occur; for, of course, its presence would be quite unnecessary in a plant which leads a submerged aquatic existence.

It does not follow, however, that this was the function in the plants of past ages. In some cases this rôle may have been performed, more especially where the parichnos occurred in the strobili. But, on the other hand, it may not hold in those cases where the tissue occurs in the vegetative leaves. In some instances, the appearance of the parichnos does warrant the assumption that it was of a secretory nature; contrariwise the facts relating to their persistence, enlargement, and lenticel-like nature in many cases favour the views held by Scott and Weiss. It may be remarked that this latter opinion is not necessarily antagonistic to the former, for it is possible that a secretory function was first performed, and, when the leaves had been shed, was followed by a respiratory rôle.

It may be remarked that if any phylogenetic value be assigned to the parichnos, then its presence in *Isoetes* gives additional support to the view that this plant belongs to the Lycopodineae. The writer is of the opinion that the parichnos has a phylogenetic value.

In conclusion, I desire to express my thanks to Dr. D. H. Scott, F.R.S., Professor F. W. Oliver, F.R.S., Mr. E. C. Jones, F.L.S., and the Authorities of the Royal Gardens, Kew, for their kindness in supplying material. It should also be mentioned that this research was commenced in the Jodrell Laboratory, Kew, and finished in the Medical School of St. Thomas's Hospital.

EXPLANATION OF PLATES XIX AND XX.

Illustrating Mr. Hill's paper on the Parichnos.

Abbreviations :—*li.*, ligule ; *p.*, parichnos ; *s.*, sporangium ; *s. m.*, sporogenous mass ; *sp.*, sporophyll ; *t.*, trabeculae ; *v.*, velum ; *v. b.* vascular bundle ; L. S., longitudinal section ; T. S., transverse section.

Fig. 1. *Isoetes Hystrix.* Diagram of T. S. through the base of the sporophyll.

Fig. 2. *Isoetes Hystrix.* T. S. through the base of a sporophyll, showing the commencement of the mucilaginous degeneration.

Figs. 3 and 4. Later stages of the same.

Figs. 5, 6 and 7. *Lycopodium clavatum.* Series of transverse sections of a sporophyll through the region of the sporangium, showing the gradual increase in the mucilaginous degeneration as the proximal end of the sporophyll is reached (Fig. 7). The three figures do not represent sections in an uninterrupted sequence.

Fig. 8. *Lycopodium clavatum.* Part of Fig. 7 more highly magnified.

Figs. 9, 10 and 11. *Lycopodium clavatum.* L. S. sporophyll and stem. Parichnos in different stages of development.

Fig. 12. *Lycopodium cernuum.* T. S. stem, showing foliage-leaves with the parichnos.

Fig. 13. *Lycopodium cernuum.* L. S. sporophyll, showing dehisced sporangium and the parichnos below.

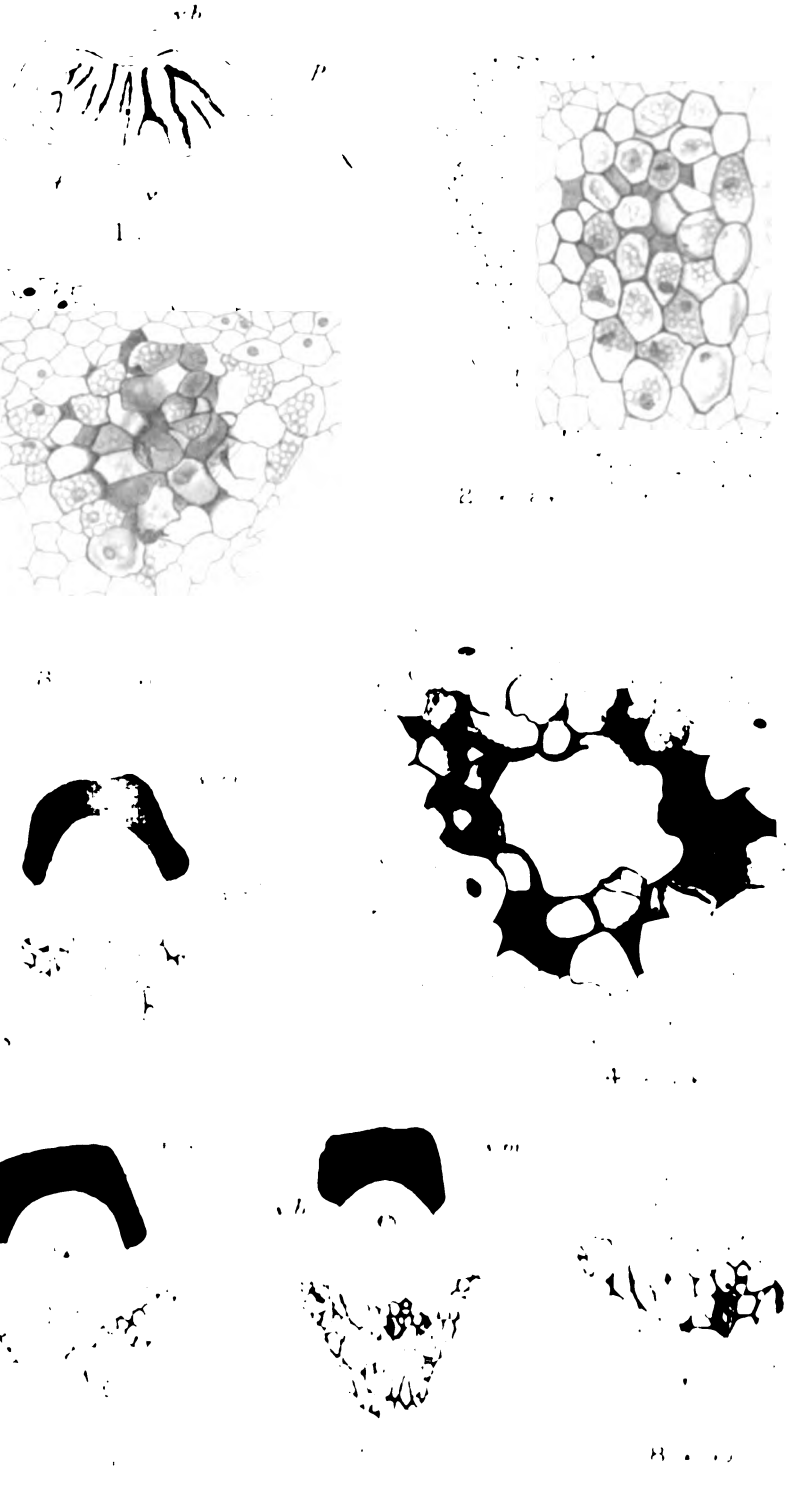
Fig. 14. *Lepidophloios* (Will. Coll., 1974 A). Photograph of part of T. S. of leaf.

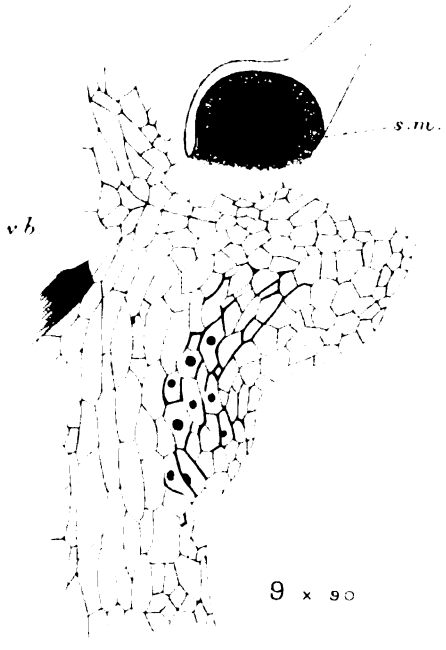
Fig. 15. *Isoetes Hystrix.* Photograph showing many sporophylls in T. S. The parichnos is seen in various stages of development.

Fig. 16. Part of Fig. 14 more highly magnified.

Fig. 17. Part of Fig. 15 more highly magnified.

Fig. 18. *Lepidodendron.* T. S. leaf, showing parichnos.





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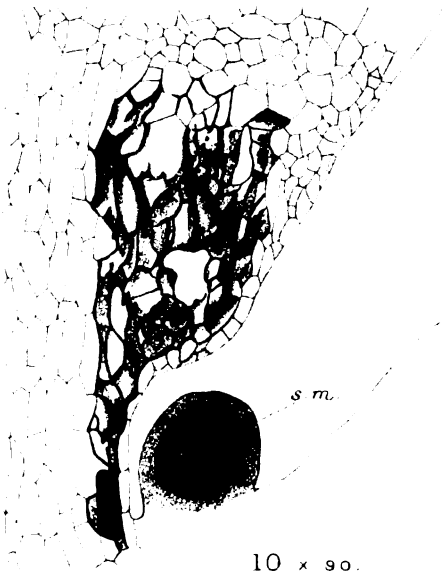

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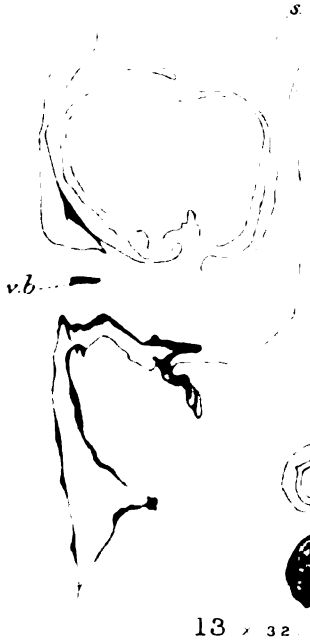

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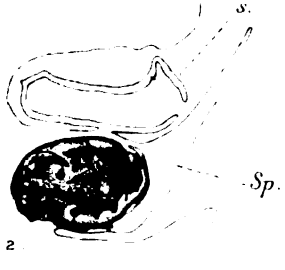

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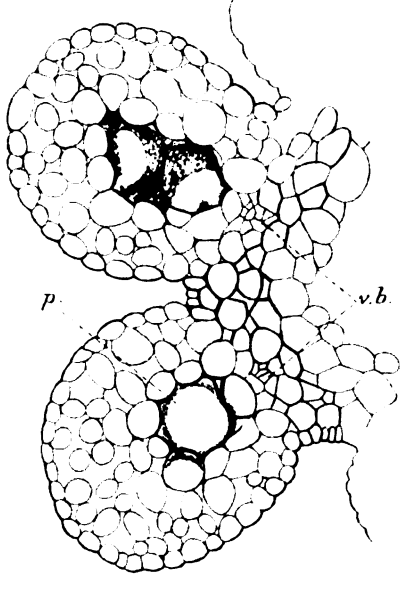

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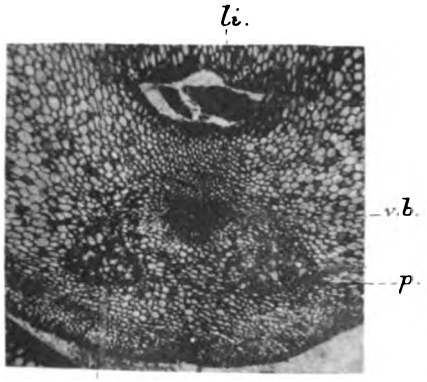

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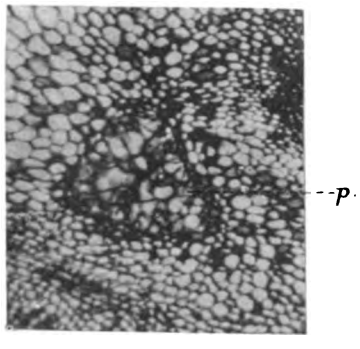

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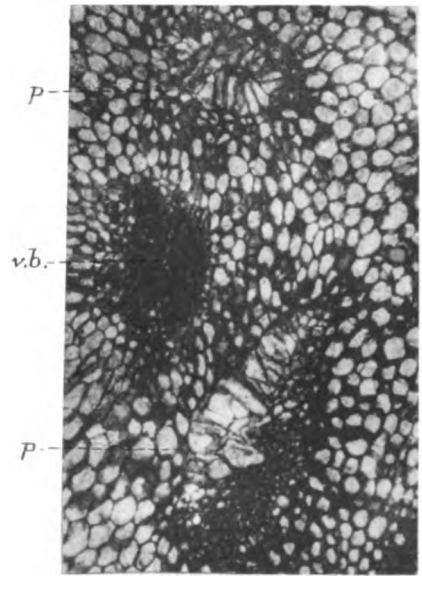

18.

On the Development of the Spores of Riccia glauca.

BY

RUDOLF BEER, F.L.S.

With Plates XXI and XXII.

THE principal facts in the development of the spores of *Riccia* have already been described by Leitgeb[1] and Strasburger[2]. In the seventeen years which have elapsed since Strasburger's paper was written botanical microtechnique has, however, made such immense progress that it was thought desirable to subject these spores to a renewed investigation. Quite recently Garber[3] has dealt with the life-history of *Ricciocarpus natans*, and Lewis[4] with the embryology and development of *Riccia lutescens* and *R. crystallina*, but neither of these authors has described the spore or the development of its membranes.

Lewis's observations show that *Riccia lutescens* is merely a terrestrial form of *Ricciocarpus natans*, and he believes that the differences which exist in the structure of the thallus and the arrangement of the sexual organs are not sufficiently marked to justify the genetic separation of *Ricciocarpus* from *Riccia*. He accordingly drops the genus *Ricciocarpus* altogether and includes *Ricciocarpus natans* among the Ricciae.

The material for the present study was fixed in strong and medium chrom-acetic mixtures (Chamberlain's formulae), strong Flemming's solution and in alcohol and acetic acid mixture. Of these the stronger chrom-acetic fluid proved the most satisfactory, but excellent results were also obtained with the alcohol and acetic mixture.

I will begin my account with the fertilization of the egg-cell. The general character of this process is shown in Pl. XXII, Fig. 28, from which it will be seen that it closely resembles the fertilization of *Riccia* (*Ricciocarpus*) *natans* as described by Garber. My photograph also shows that the shrinkage

[1] Leitgeb, Ueber Bau und Entwicklung der Sporenhäute. Graz, 1884, pp. 39–49.

[2] Strasburger, Ueber das Wachsthum vegetabilischer Zellhäute. Histologische Beiträge, Heft 2, 1889, pp. 104–11.

[3] Garber, The Life-history of *Ricciocarpus natans*. Bct. Gazette, vol. xxxvii, 1904, pp. 161–77.

[4] Lewis, The Embryology and Development of *Riccia lutescens* and *Riccia crystallina*. Bot. Gazette, vol. xli, 1906, pp. 109–38.

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of the egg-cell is far less than is usually figured, and in this point I am again in agreement with Garber's statements. The first division of the fertilized egg-cell is usually obliquely transverse (Fig. 32). The succeeding divisions have been so frequently described that I need not recapitulate them here. They result in a mass of sporogenous tissue surrounded by a single layer of sterile wall-cells, the whole being enclosed within a two-layered calyptra. The young spore-mother-cells are at first separated from one another by extremely delicate membranes (Fig. 29). These stain, often deeply, with bismarck brown, but I am unable to get a decided reaction in them with ruthenium red, whilst with calcium-chloride-iodine and chlor-zinc-iodine they colour yellow but show no signs of containing cellulose.

The cell contains a quantity of starch which is especially abundant round the nucleus. Upon the primary walls which separate the spore-mother-cells from one another a secondary and, later, a tertiary thickening layer is deposited (Pl. XXI, Fig. 5). Both layers give the reaction of cellulose as well as those of pectose, but the tertiary thickening layer (viz. the one in immediate juxtaposition with the protoplast) stains the more deeply with pectic reagents.

The protoplast surrounded by the tertiary thickening layer now rounds itself off and becomes separated from the primary mother-cell membrane. The secondary thickening layer, which has become more or less mucilaginous in consistency, sometimes separates completely from the primary walls and then forms a well defined layer surrounding the protoplast (Figs. 5, 9, 31). At other times, on the contrary, it remains partly adherent to the primary wall and in that case it becomes drawn out into a number of strands bridging over the gap between the rounded protoplast and the primary wall. The latter condition is represented in Fig. 6, and it will be observed that my drawing closely resembles Leitgeb's Fig. 3, Taf. II. Leitgeb, however, believed that the space between the primary wall and the protoplast was occupied by a homogeneous mucilage, and that the strands of material which both he and I have figured are composed of food-materials diffusing in from the outside. In my preparations it is quite certain that no homogeneous mucilage occupies the space between protoplast and primary wall; moreover the strands of material stretching across this space give cellulose and pectose reactions exactly corresponding with those obtained in the secondary thickening layer (e.g. of Fig. 5 where the cells are still partly united).

It should be mentioned that the condition represented in Fig. 6 is no doubt somewhat exaggerated by the reagents used. The measurement of the spore-mother-cells shown in Figs. 30 and 9 gave an average diameter of about 46 μ, whilst that of the cells in the sporangia from which Fig. 6 was drawn was only 40 μ. I believe, therefore, that the effect is somewhat heightened by the reagents employed, but I see no reason to conclude that

the condition is entirely due to them. During the isolation of the spore-mother-cells from one another the sporangial cavity enlarged considerably. Taking the measurements from the periphery of the outer of the two layers of the archegonial wall the diameter of the cavity at such a stage as that shown in Fig. 29 is about 240 μ, whilst when the mother-cells are rounding off (as in Fig. 30) it has increased to about 300 or 345 μ.

Garber and Lewis have both described a large amount of nutritive material which fills the space between the mother-cells and which is secreted by the surrounding cells. In my preparation of *Riccia glauca* I have seen nothing of this material [1].

The rounded mother-cells now proceed to divide. The following description is based upon the study of preparations which have been stained with Heidenhain's haematoxylin, either alone or with a light counter stain with bismarck brown. The large nucleus of the spore-mother-cell just before the commencement of division contains a conspicuous, deep-staining nucleolus and a number of delicate linin fibres which have little affinity for dyes (Figs. 1 and 2). In these features the resting nucleus of the sporogenous cells of *Riccia glauca* differs from the description given by Lewis for the two species which he has studied. He found the nuclear cavity to be occupied by a linin network upon which the scanty chromatin is irregularly scattered; moreover he states that no nucleolus was to be seen. I have examined a large series of sections of sporangia containing mother-cells at all stages up to their maiotic division, but I have never observed a nucleus which contained a reticulum such as Lewis figures, nor one which was without a nucleolus. In the case of *Riccia glauca*, therefore, we can be certain that no such non-nucleolated, reticular resting stage occurs.

It may also be added that the resting condition of the vegetative nuclei of the thallus of *Riccia glauca* agrees essentially with what I have described above in the case of the sporogenous cells.

The nucleolus in nearly all cases has a lobular outline (Fig. 1) and I believe that this is due to the fact that the nucleolus is not a homogeneous body, but is composed of a number of small chromatic masses or granules held together by a common matrix. These granules are usually so closely crowded together in the nuclei of the sporogenous cells that it is not easy to see their separate individuality. In a few cases, however, the nucleolus was actually seen to be composed of distinct granule-like bodies which had become rather more widely separated from one another than usual by the action of the reagents employed or through the pressure of the microtome knife (Fig. 2) [2]. In the vegetative nuclei at the growing apex of the thallus the constitution of the nucleolus can be much more readily determined when

[1] See Garber, l. c., Plate X, Fig. 37.

[2] Compare also Fig. 16, in which the separate chromatin granules of the earlier stages of division are massing together to form one body.

differentiation with the iron-alum has been carried to the right point. It can then be seen that these nucleoli consist of a faintly stained matrix in which are embedded a number of intensely black bodies (Fig. 3).

Compound nucleoli of a similar character occur in the nuclei of the Musci. In the spermatogenous cells of *Atrichum undulatum* the nucleoli can be quite clearly seen to consist of a lightly coloured matrix containing a number of chromatic particles [1].

In several sporangia I have found that the linin threads tend to become more or less massed towards one side of the nuclear cavity (Fig. 7). This may correspond to a synapsis stage, although I am not prepared to say how far reagents are responsible for its production in the present case.

Following this condition we find that a much more deeply staining and thicker thread has been developed, which traverses the nuclear cavity in a number of coils or loops (Fig. 8). This is unquestionably the spirem-thread, and it differs radically from the short thread described by Lewis in *Riccia crystallina* [2]. The thread can often be followed continuously for a considerable distance, and I believe that it forms an unbroken filament.

In well stained preparations the spirem-thread shows very beautifully an alternation of deeply coloured bodies (chromomeres) with lighter areas (Fig. 8).

It is very probable that the increased amount of chromatic material which the thread contains at the spirem stage has been derived from the nucleolus and most likely at the expense of the chromatic granules which this body encloses. I have unfortunately been unable to find the stages in the division of the sporogenous cells which lie between the establishment of the spirem and the arrangement of the chromosomes at the equator of the spindle (Fig. 10). In the spermatogenous cells of the antheridium, however, in which a spirem is also developed, the actual segmentation of this thread into the chromosomes could be followed, and it was clearly seen that during this process the nucleolus became more and more inconspicuous. By the time the chromosomes are fully established the nucleolus has been lost sight of altogether.

Both Garber and Lewis have recorded four chromosomes in *Riccia* (*Ricciocarpus*) *natans*, and Lewis found the same number in *Riccia crystallina*. In *Riccia glauca* the number of chromosomes is higher than this, and I have been able to determine with certainty that the reduced number is either seven or eight (Figs. 9 and 11). The distribution of the chromosomes to

[1] I should like to take this opportunity of correcting an error which I made in a previous note upon 'The chromosomes of *Funaria hygrometrica*' (New. Phyt., vol. ii, 1903, p. 166). I there stated that the number of chromosomes which appeared in the first division of the spore-mother-cells was four. Since this was written I have examined properly fixed material of several mosses (*Funaria hygrometrica*, *Atrichum undulatum*, *Mnium hornum*, *Polytrichum juniperum*) and I have found that in all cases the number of chromosomes is far higher than I formerly supposed.

[2] Compare Lewis's Plate VII, Fig. 35, with my drawing of this stage.

the daughter-nuclei is shown in Fig. 11. On first reaching the apex of the spindle the chromosomes are crowded closely together (Fig. 12). Soon, however, a nuclear membrane is formed and the chromosomes proceed to open out.

During the earlier stages of the telophase a number of chromatic bodies can be seen distributed upon the linin, and these bodies are no doubt the derivatives of the chromosomes (Figs. 13 and 14). At a later stage the scattered chromatin bodies have come together to form a single lobular nucleolus, whilst linin fibres, containing little or no stainable material, extend through the nuclear cavity (Figs. 15 and 16). The spindle during the metaphase and anaphase of the division is a comparatively narrow structure. A conspicuous cell-plate is developed at the equator of the spindle (Fig. 12). During the telophase of division the spindle shortens and broadens out very considerably and the cell-plate becomes correspondingly broader (Fig. 14).

A membrane is developed at the equator of the spindle, no doubt between the split halves of the cell-plate, although the splitting of the plate could not be followed here on account of its great delicacy. This membrane, which stains rather deeply with bismarck-brown, does not at first reach right across the cell (Fig. 15), but by the time that the nuclei are again dividing it has almost or quite reached the periphery of the cell (Fig. 17). After a short interval of rest the nuclei enter upon the second maiotic division.

At the conclusion of this division cell-membranes are formed which complete the division of the mother-cell into the four daughter-cells, which are conveniently, if incorrectly[1], called the special-mother-cells. These membranes, separating the special-mother-cells from one another, give both cellulose and pectose reactions, as do the secondary and tertiary thickening layers of the mother-cell which still form the peripheral envelope of the tetrad group.

It may be mentioned here that during the development of these septa a large proportion of the starch of the cell is seen to be aggregated in their neighbourhood (Figs. 17 and 18).

The special-mother-cell walls do not long remain in this condition, but secondary thickening layers are soon deposited upon the inner surfaces of the thin pectose-cellulose membranes (Fig. 19).

These thickening layers have an uneven outline, forming the papillate projections into the interior of the cell, which previous writers have fully described. Their reactions show that they consist of callose apparently unaccompanied by any other substance. They colour deeply in corallin-soda, in aniline-blue, in congo-red and in naphthol-black[2]. On the other

[1] Miss Benson, New Phytologist, vol. iv, 1905, p. 96.

[2] I have elsewhere dealt with the specific staining properties of naphthol-black (see Beihefte zum Bot. Centralblatt, Bd. XIX, Abt. I, Heft 2, 1905, p. 289).

hand, calcium-chloride-iodine and chlor-zinc-iodine do not stain these layers. In ruthenium-red and bismarck-brown they assume a faint colour, but I do not think that this is sufficiently marked to indicate the presence of pectose in these layers.

The membranes which first limited the cells of the tetrad from one another before the thickening layers were deposited can now be seen as middle lamellae running through the midst of the callose layers, and as a peripheral covering to the entire tetrad. These primary membranes continue to colour distinctly pink-violet with calcium-chloride-iodine solution and deeply red with ruthenium-red, whilst callose reagents leave them unstained. They still possess, therefore, the unchanged pectose-cellulose constitution which they had in the first place.

It may be mentioned here that Leitgeb[1] reached very different results on these points. During the earlier stages following the thickening of the special-mother-cell walls he could distinguish no middle lamella, and only after the first spore-wall has made its appearance 'differenzirt sich in den Scheidewänden die Mittellamelle.' This is certainly incorrect, for the middle lamellae are nothing but the original pectose-cellulose septa of the unthickened special-mother-cell wall which maintain their individuality throughout.

Leitgeb further states, on the same page, that in aniline-blue an outer layer of the special-mother-cell wall colours deep blue whilst the inner parts, corresponding to our secondary thickening layers, only assume a yellowish tinge in this solution. If this were the case we should have to conclude that the composition of the special-mother-cell wall is very different from that which I have described above, but I have so repeatedly assured myself that the behaviour of this wall towards aniline-blue is precisely the opposite to what Leitgeb found and, moreover, this has been so thoroughly supported by the reactions of the wall with other reagents, that there cannot be the slightest doubt of the correctness of my conclusions.

The occurrence of callose in the special-mother-cell walls of one of the Hepaticae is of interest since in no other member of the Archegoniate series which I have examined is that substance to be found in this position; and it is only when we reach the Gymnosperms and Angiosperms that callose can again be seen surrounding the pollen-tetrads[2].

It is very probable that callose occurs constantly in the special-mother-cell walls of the liverworts since some observations which I am making upon the spore-development of *Anthoceros laevis* have shown that callose is also present in the tetrad walls of this plant.

In the Musci the special-mother-cell walls contain pectose and cellulose,

[1] Leitgeb, l. c., p. 43.

[2] In all Gymnosperms and Angiosperms which I have examined callose formed the only demonstrable constituent of the special-mother-cell wall.

whilst in the leptosporangiate ferns, the Ophioglossaceae and in the ligulate and eligulate Lycopodiums these walls contain either cellulose and pectose or pectose alone, but no trace of callose[1]. On another occasion[2] I have referred to the manner of origin of callose in the special-mother-cell walls of *Oenothera*, and the same remarks apply with equal force to the callose of *Riccia*. In the present case it is impossible to suppose that the callose can have arisen from the transformation of cellulose, since none of this substance precedes the callose nor can any cellulose be seen to disappear from other neighbouring membranes. We must conclude, therefore, that the callose in the tetrad walls of *Riccia* is formed directly as such by the protoplast.

The tetrad-group grows in size from about 60 μ to about 75 to 85 μ in diameter and then the first spore-wall[3] is formed round each of the four cells. The question of the origin of this layer constitutes one of the chief points of difference between the accounts of Leitgeb and Strasburger. The former writer was convinced that this wall is a transformation product of the innermost layers of the special-mother-cell wall, whilst Strasburger is equally positive that it is a new formation of the protoplast which has no relation to the special-mother-cell wall.

I have spent no little time upon this question and the only conclusion which I am able to reach is a negative one. After carefully considering the grounds upon which Leitgeb and Strasburger based their respective views I am forced to conclude that these were insufficient to prove the case either one way or the other. Leitgeb lays the greatest weight upon the firm adhesion which exists between the special-mother-cell wall and the first spore-wall. After treating the spores with various reagents (chlor-zinc-iodine or a not too strong mixture of chromic and sulphuric acids) he found that the first spore-wall remained firmly fixed to the special-mother-cell wall, although this was greatly swollen.

An argument based upon the adhesion of two layers to one another cannot, however, be accepted as proof of their common origin. Cases are known in which two layers are firmly united but which have unquestionably been separately deposited by the protoplast. Thus Fitting[4] has referred to the special-mother-cell wall and the secondary thickening layer of the spore-mother-cell wall of *Isoetes* which adhere closely together but which are independently developed. The special-mother-cell wall and the very young pollen-wall of the Phanerogams furnish another example of two layers which

[1] I have, unfortunately, had no opportunity of examining the special-mother-cell walls of *Equisetum* as yet.

[2] Beer, l. c., p. 290.

[3] In the following account I have avoided the terms exospore or perispore and speak only of first and second spore-membranes. Since, however, the innermost layer of the spore is certainly homologous with the endospore of other plants I have used that name for it.

[4] Fitting, H., Bot. Zeit., Bd. 58, 1900, p. 126.

are often at first inseparably united, but which nevertheless have a distinct origin. In his examination of *Riccia* Strasburger found that by bursting the special-mother-cell wall by means of pressure he was able to separate the spore-protoplast, surrounded by the first spore-wall, from the special-mother-cell wall. Moreover, he states that the folds of the first spore-wall never quite reach to the summits of the indentations in the special-mother-cell wall [1]. If this were actually the case it would, as Strasburger clearly saw, form strong evidence in favour of the independent origin of the two layers. My own preparations, however, do not confirm Strasburger in this respect. Wherever the section is accurately longitudinal (as regards the fold of membrane and the indentation) it can be distinctly seen that the first spore-wall lines the indentation in the special-mother-cell wall to its very apex. Where, however, the section has cut the fold of the first spore-wall somewhat obliquely the true relations of this fold to the indentation are not always at once clear.

From what has been said above it will be seen that the evidence which we possess is entirely inconclusive and that neither Leitgeb nor Strasburger were justified by the facts in assuming a definite position.

A study of the microchemical reactions of this wall furnishes no assistance in deciding this question. The whole behaviour of the wall indicates that it is cuticularized from a very early period; whether there is a basis of cellulose, callose, or pectose preceding or underlying the cuticularization was not apparent from any of my experiments.

It may be mentioned here that after treating sections of older spores with a mixture of chromic and sulphuric acids and then (after washing) adding chlor-zinc-iodine it can be seen that the first spore-wall has a rather densely laminated structure (Figs. 24 and 25).

Not long after the first spore-wall has been formed a deposit of mucilaginous substance can be seen at the equatorial rim [2] of the spore (Fig. 20). As Leitgeb correctly stated, this mucilage has the same chemical and physical properties as the secondary thickening layers of the special-mother-cell wall; that is to say it is composed of callose. Leitgeb further supposed that this mucilage was derived from the special-mother-cell wall, a portion of which wandered through the first spore-wall at the equatorial region. The first spore-wall is, however, always continuous and never interrupted at any spot, as Leitgeb thought was sometimes the case (Figs. 20, 21). Strasburger considered the mucilage to be a part of the first spore-wall; his chief reason for doing so was that he found that this wall and the mucilage were not sharply marked off from one another at the equatorial rim. I find that the mucilage is formed later than the first spore-wall, that the callose

[1] Strasburger, l. c., p. 109.

[2] Leitgeb called this equatorial rim a 'Saum,' whilst Strasburger wrote of 'einem äquatorialen Flügel, das heisst einem an der Grenze von Rücken- und Bauchfläche verlaufenden Saum.'

mucilage is always sharply defined from the delicate spore-wall which has quite different staining properties, and that it is not difficult to separate the one from the other by means of reagents. I regard the mucilage, therefore, as a new formation which has no relation either to the special-mother-cell wall or to the first spore-wall.

The older writers believed that this mucilage formed a continuous layer over the inner face of the first spore-wall. I do not find this to be the case.

Over the ventral surfaces of older spores, in which the second spore-wall has been developed, it can be seen that the two membranes lie closely against one another without any mucilage between them (Fig. 21). Over the dorsal surface of the spore the two layers of the wall are indeed frequently separated from one another and then the space between them appears to be, at least partly, occupied by a mucilage. How far this separation between the two walls of the spore over the dorsal surface is a normal feature of their structure is, however, difficult to say. In older spores the mucilage at the equatorial rim has again become absorbed and can no longer be seen.

At first this mucilage is limited internally only by the plasma membrane of the protoplast, which is pushed inwards at the equatorial seam by the plug of mucilage (Fig. 20). Before long, however, the spore-protoplast develops a new wall within the first one, and this then forms a flattened internal boundary to the mucilage at the rim of the spore (Fig. 21). This second spore-wall is a cuticularized structure almost from the commencement. At the very first, however, it is probably composed of uncuticularized pectose-cellulose, for when it is just discernible it stains more deeply with bismarck-brown than is usual with cuticularized membranes, and, moreover, the lamellae which are subsequently added to its thickness unquestionably have, at first, a pectose-cellulose constitution.

During the earliest stages of its existence the second spore-wall appears, even under high magnifications, as a perfectly homogeneous layer, but in spores which are a little older it has become considerably thicker and then a dark line can be seen traversing the middle of this wall and dividing it into an inner and an outer part (Figs. 22, 35). This dark line grows in thickness with the age of the spore until it not infrequently becomes a thick layer which stains intensely black with Heidenhain's haematoxylin and forms the most conspicuous feature in the spore-wall (Fig. 26). It is not easy to assure oneself of the real nature of this dark layer, but after comparing together a large number of spores I am led to the conclusion that this layer most probably only represents a gap which is formed between two sets of lamellae and which becomes occupied by some dark-coloured, stainable material. This view seems to me to be supported by the fact that the dark layer varies in the time and in the position of its appearance. Some-

times it is discernible at a very early stage in the history of the second spore-wall. Sometimes the spore has become much older and the second spore-wall has become quite a thick structure before any signs of this layer can be seen[1]. Again its appearance is sometimes nearer, sometimes further away from the outer periphery of the spore-wall. In preparations which have been treated with a mixture of chromic and sulphuric acids a separation of two sets of lamellae can often be seen in the second spore-wall with an evident gap between them. Further evidence is given by a study of older spores in which a similar but much narrower black band can usually be seen between the inner boundary of the second spore-wall and the endospore (Fig. 26). What the nature and origin of the substance which occupies this space may be is quite unknown. It does not seem unlikely, however, although I can bring forward no proof for the view, that the dark substance which collects in the gap of the spore-wall is the material which colours brown the older spore-walls throughout their thickness.

Most instructive preparations of the spore-wall at the middle periods of development may be obtained by treating sections with a mixture of chromic and sulphuric acids, washing and then examining them in chlor-zinc-iodine or calcium-chloride-iodine. The first spore-wall is coloured yellow and shows a densely laminated structure. Within this wall lies the second spore-wall. The outer portion of this wall is seen to be composed of loosely arranged lamellae which sometimes lie closely against the first spore-wall but which have usually become separated from it by the action of the reagent (Figs. 24, 25). The inner portion of the wall, which is generally separated from the loose lamellae by a gap, has a homogeneous appearance and no lamellae can be distinguished in it. If the action of the acids has been carried to the right point it can be seen that the inner part of this internal layer of the second spore-wall gives beautiful cellulose reactions with the iodine reagents. The band of cellulose is considerably thicker on the dorsal surface of the spore, whilst cuticularization had become more complete over the ventral surfaces. Congo-red in dilute solution also colours the cellulose areas a deep red.

Although the inner portion of the second spore-wall has a homogeneous appearance, even after the action of reagents, it is nevertheless really built up of successive lamellae.

During the development of the spore this inner region of the second spore-wall grows very considerably in thickness, and the sections show with unmistakable clearness that this growth is due to the deposition of a series of lamellae upon one another. The newest lamella is formed by the protoplast of the spore in the most intimate attachment with the plasmatic membrane. By plasmolysing the protoplast this lamella is usually at the same time separated from the walls of the spore and the contracted proto-

[1] The late appearance of this dark layer is shown in Fig. 23.

plast can then be seen to be surrounded by a thin layer which gives cellulose-pectose reactions (Fig. 36). It may be said, therefore, that in the formation of the second spore-wall the first lamellae which are deposited are comparatively loosely arranged together (outer region of second spore-wall), whilst the later ones become so firmly united that the lamellose nature of this portion of the wall becomes obscured (inner region of second spore-wall). It is these two regions of the wall—the loosely and the densely laminated areas respectively—which become more or less separated from one another by the interpolation of the dark material which was mentioned above.

The endospore is formed comparatively late in the development of the spore. It gives the reactions of cellulose and pectose, and it is usually separated from the second spore-wall by a narrow space occupied by dark material similar to that which occurs in the more conspicuous gap between the two layers of the second spore-wall (Fig. 26). In spores which are nearly or quite mature the walls are deeply coloured brown and have become much denser and in consequence thinner. The lamellated structure of the wall is now obscured. Heated to redness on platinum foil with a drop of concentrated sulphuric acid the entire spore dissolves without leaving a silica skeleton behind.

Nothing has been said above of the nutrition of the spore or of the sources of the material for the growth of its membranes, so that a few words upon this subject must be added here. That the protoplast of the spore is itself actively concerned in the growth of the membranes which surround it can scarcely be doubted. The new lamellae which are added to the second spore-wall are formed, as we have seen, in the most intimate union with the plasmatic membrane; the nucleus of the spore also presents an appearance which strongly suggests that it is participating in metabolic activities.

Unlike the usual resting nucleus of *Riccia glauca*, to which I have already referred, the chromatin is not confined to the nucleolus, but is also distributed along a rather thick filament which strongly recalls the spirem-thread of the dividing nucleus (Fig. 27 *a*, 27 *b*). It is difficult to decide whether this thread forms one continuous structure or not.

As the spore grows older and its walls become thickened we find that, although the thread long maintains its spirem-like arrangement, it gradually stains less and less deeply with the haematoxylin (Fig. 27 *c*). Somewhat similar spirem-nuclei have been described in various animal cells. Thus the well-known case of the salivary glands of *Chironomus* larvae, studied by Balbiani, may be recalled, or the ovarian eggs of *Triton taeniatus*, in which Born found a spirem-stage to precede a more diffuse arrangement of the chromatin. In most of the cases already known in which the chromatin is distributed through the nucleus in this manner, we are dealing with cells

which exhibit considerable metabolic activity, and we may probably infer that some relation exists between the spirem-arrangement and the cell activity. A similar relation between the peculiar nuclear structure and cell-metabolism no doubt also occurs in the developing spores of *Riccia glauca*. The actual material which is used by the protoplast in forming and adding to the spore-walls must be derived from without the spore. The reserve material and cytaplasm of the spore suffer very little diminution during development, and if these are drawn upon to furnish material for the growth of the membranes, this loss is at once fully compensated by the arrival of new material from without. The starch-contents of a spore at about the middle period of its development is shown in Fig. 34, and almost precisely the same appearance is presented by the spore-protoplast in the preceding and succeeding stages.

Both the sterile parietal layers of the sporangium and the inner layer of the calyptra[1] degenerate and yield some material which is no doubt employed in the growth of the spore-walls. Neither of these layers is, however, rich in substance (see Figs. 4, 29), and I scarcely think it is possible that their degeneration can furnish all the material required for the very considerable growth undergone by the membranes. Most probably this source is supplemented by material which is assimilated by the vegetative cells of the thallus, and which diffuses into the sporophyte in a state of solution. After the first spore-wall has been formed, and during all the earlier periods of the growth of the second spore-wall, a mucilage is constantly present in the sporangium between the spore-tetrads (Fig. 33). The origin and significance of this mucilage are, however, somewhat obscure. It is certainly not the material secreted by the surrounding cells of the thallus, since not a trace of mucilage can be detected in any of these. The callose special-mother-cell walls, which for some time continue to surround the spore-tetrads, gradually disappear, but there is no evidence to show that their substance makes any contribution to the sporangial mucilage which, moreover, gives none of the reactions of callose. Two sources remain, both or either of which may be responsible for the sporangial mucilage. In the first place the degeneration of the parietal cells of the sporangium and of the inner archegonial layer may contribute to the formation of the mucilage. In that case it still remains to be explained how it is that the parietal cells have degenerated some time before the mucilage can be seen, whilst some remains of the inner archegonial cells can frequently still be detected after the mucilage has again become absorbed. Secondly, the degeneration of the primary mother-cell walls and of their thickening layers, which are both lost sight of about this time, may give rise to part or all of the sporangial mucilage. A difficulty in the way of at once accepting this view of the origin of the

[1] The outer layer of the calyptra persists to a very late stage.

mucilage lies in the fact that whilst the secondary thickening layer of the mother-cell walls gives both cellulose and pectose reactions, I have been unable to demonstrate the presence of cellulose in the mucilage.

It must, therefore, remain uncertain for the present to what extent the mucilage in the sporangium possesses a nutritive value.

By the time that the second spore-wall has become differentiated into the two sets of lamellae (with the dark layer separating them from one another) the mucilage has become very scanty, and soon after it entirely disappears.

SUMMARY.

1. Fertilization of the egg-cell of *Riccia glauca* corresponds essentially with Garber's description of this process in *Riccia* (*Ricciocarpus*) *natans*.

2. The spore-mother-cells are at first separated from one another by extremely delicate membranes, which stain deeply with bismarck-brown but in which no cellulose could be demonstrated.

3. Upon these primary spore-mother-cell walls secondary and, later, tertiary thickening layers are deposited. Both these layers give pectose-cellulose reactions.

4. The protoplast, surrounded by the tertiary thickening layer, now rounds itself off. The secondary thickening layer, which becomes more or less mucilaginous, sometimes separates completely from the primary wall and then forms an external envelope to the mother-cell, whilst at other times it still remains partly adherent to the primary wall, and in that case it becomes drawn out into strands of mucilage bridging over the space between primary wall and tertiary thickening layer. The latter condition corresponds to Leitgeb's description of this stage, but he erroneously interpreted the mucilage-strands as nutritive material passing into the mother-cell.

5. In *Riccia glauca* no demonstrable nutritive material was found between the isolated mother-cells such as Garber and Lewis have described in the case of *Riccia* (*Ricciocarpus*) *natans*.

6. The resting nucleus of the spore-mother-cell contains a large, deep-staining nucleolus and a number of delicate linin fibres. No non-nucleolated, reticular resting nucleus, as described by Lewis in *Riccia* (*Ricciocarpus*) *natans* and *R. crystallina*, was found in *Riccia glauca*.

7. The nucleolus of the nucleus of *Riccia glauca* appears to be a compound structure consisting of a number of deeply chromatic masses or granules embedded in a matrix which stains only faintly.

8. A long and well-marked spirem-thread occurs in the prophase of the division of the spore-mother-cell. This differs radically from the short thread described and figured by Lewis in *Riccia crystallina*.

9. The reduced number of chromosomes in *Riccia glauca* is either seven or eight, but it could not be decided with certainty between these two numbers.

It will be noted that this number is considerably higher than that (four) recorded by Garber and Lewis in *Riccia* (*Ricciocarpus*) *natans* and *R. crystallina.*

10. In the telophase of the division a number of chromatic bodies, which are no doubt derivatives of the chromosomes, are distributed upon the linin fibres. Subsequently these scattered bodies aggregate together to form the lobular nucleolus of the resting nucleus.

11. The membrane, which is formed between the daughter-cells resulting from the first division of the mother-cell, does not at first extend to the periphery of the cell.

12. At the conclusion of the second maiotic division the special-mother-cells are separated from one another by delicate membranes which have a pectose-cellulose composition.

13. Upon these primary special-mother-cell walls secondary thickening layers are deposited which give the reactions of callose. This callose is directly deposited as such by the protoplast, and is not a transformation product of cellulose.

14. The first spore-wall is a cuticularized structure from a very early period. No decisive data could be found to determine whether this wall is derived from the transformation of the innermost lamellae of the special-mother-cell wall or whether it is a new formation directly due to the secretory activity of the protoplast. It was shown that the arguments brought forward by previous writers are insufficient to prove the case either one way or the other.

15. Within the first spore-wall at the equatorial rim a plug of mucilage is deposited. This mucilage, which gives the reactions of callose, has no direct relation either to the thickening layers of the special-mother-cell wall (as Leitgeb supposed) or to the first spore-wall (as Strasburger supposed). It is a new and independent formation.

16. The second spore-wall is next formed within the first wall. It is cuticularized from a very early time, but there is reason to believe that previous to its cuticularization it reacts as a pectose-cellulose membrane.

17. At first the second spore-wall appears to be quite homogeneous, but subsequently it can be seen to be composed of three parts:—

(i) an external loosely laminated region;
(ii) a layer of dark-coloured material; and
(iii) an internal densely laminated region.

The dark-coloured material appears to have been interpolated into a space which forms between the two laminated regions of the wall.

18. The endospore, which is formed late in the development of the

spore, gives the reactions of pectose and cellulose. It is often separated from the second spore-wall by a very thin band of dark-coloured material similar to that which occurs in the gap between the two regions of the second spore-wall.

19. No silica could be detected in the spore-membranes.

20. The protoplast of the spore is actively concerned in the growth of the membranes which surround it. The intimate union which exists between each new lamella, which is being added to the wall, and the protoplast in itself indicates this fact, whilst the curious spirem-like structure of the spore-nucleus, resembling that of certain animal cells, also suggests the occurrence of active metabolic processes in the cell.

21. The actual material necessary for the growth of the spore-walls is partly derived from the breaking down of the parietal cells of the sporangium and of the inner layer of the calyptra. This source is most probably supplemented by material which is assimilated by the vegetative cells of the thallus, and which diffuses into the sporophyte in a state of solution.

22. After the first spore-wall has been formed, and during all the earlier periods of the growth of the second spore-wall, a quantity of mucilage is constantly present in the sporangium between the spore-tetrads. The origin and significance of this mucilage are, however, still somewhat obscure. The various possibilities of the case are discussed in the body of the paper.

In conclusion I should like to express my thanks to Professor J. B. Farmer, F.R.S., for kindly examining my sections and for offering several valuable suggestions.

EXPLANATION OF FIGURES IN PLATES XXI AND XXII.

Illustrating Mr. Beer's paper on the Spores of *Riccia*.

All Figures refer to *Riccia glauca*.

PLATE XXI.

A. DRAWINGS.

Fig. 1. Spore-mother-cell. Resting nucleus showing lobular nucleolus.

Fig. 2. Spore-mother-cell. Nucleolus of resting nucleus broken up into distinct granules.

Fig. 3. Nucleoli of nuclei from the apex of the thallus showing chromatic granules embedded in a matrix.

Fig. 4. Sterile parietal cells of sporangium in which the mother-cells were becoming rounded off.

Fig. 5. Spore-mother-cells which are separating from one another. Where they are still attached a middle lamella (the primary wall) and secondary and tertiary thickening layers can be recognized. × about 1100.

Fig. 6. Spore-mother-cell which is becoming rounded off. Secondary thickening layer forms strands between primary wall and tertiary thickening layer. × about 1100.

Fig. 7. Spore-mother-cell. Synapsis (?).

Fig. 8. Spirem-stage of the first division of the spore-mother-cell. × about 1100.

Fig. 9. Chromosomes at equator of spindle. Secondary and tertiary thickening layers of the wall surround the spore-mother-cell.

Fig. 10. Chromosomes at the equator of the spindle in first division of the spore-mother-cell. × about 1100.

Fig. 11. Anaphase of first division of the spore-mother-cell. × about 1100.

Fig. 12. Chromosomes crowded together at the poles of the spindle. × about 1100.

Fig. 13. Telophase of first division of the spore-mother-cell. × about 1100.

Fig. 14. Later stage of telophase.

Fig. 15. Daughter-nuclei in resting condition before commencement of second division. Septum between cells not yet complete.

Fig. 16. Daughter-nucleus from similar cell as in Fig. 14. Chromatin granules are aggregating together to form the compound nucleolus.

Fig. 17. Second division of the spore-mother-cells. The septum between the cells now nearly or quite reaches the periphery. × about 1100.

Fig. 18. Young tetrad with delicate septa between the cells and the periphery still clothed with secondary and tertiary thickening layers of mother-cell-wall.

Fig. 19. Special-mother-cells. Examined in glycerine and congo-red. Thickening layers red; middle lamellae and periphery colourless.

Fig. 20. Spore with first spore-wall (drawn black) at the equatorial rim of the spore. Examined in glycerine and congo-red. Secondary thickening layers of special-mother-cell and mucilage at the rim of spores (both left white in the figure) stained red; spore-wall yellowish. Equatorial mucilage limited internally by the plasma membrane alone. × about 1100.

Fig. 21. Spore with first and second spore-walls in the neighbourhood of the equatorial rim. The second spore-wall still appears homogeneous. Examined in glycerine containing a very little fuchsin.

Fig. 22. Spore at the equatorial rim. Early stage in the differentiation of the second spore-wall.

Fig. 23. Older spore. Examined in calcium-chloride iodine. Second spore-wall differentiated into an outer distinctly laminated region and an inner apparently homogeneous region. In the present case the darkly coloured layer is only just appearing between the two regions at this comparatively late stage.

Fig. 24. Portion of spore-wall after warming in a mixture of chromic and sulphuric acids, washing and examining in calcium-chloride-iodine solution. Laminated structure of first spore-wall and outer region of second spore-wall is well shown. Intimate union exists between remains of thickening layers of special-mother-cell walls and first spore-wall. Both first and second spore-walls colour yellow. × about 1100.

Fig. 25. Somewhat older spore treated similarly to the one drawn in Fig. 24. All the membranes colour yellow. × about 1100.

Fig. 26. Older spore from microtome section stained with Heidenhain's haematoxylin and bismarck-brown. Dark-coloured layer between inner and outer regions of the second spore-wall is very conspicuous. A similar, but narrow, dark layer lies between the second spore-wall and the endospore. × about 1100.

Fig. 27. Nuclei from developing spores:

(*a*) from spore with first spore-wall only;

(*b*) from spore with two spore-walls but second wall still homogeneous;

(*c*) from older spore with thick, differentiated second spore-wall.

PLATE XXII.

B. PHOTOGRAPHS.

Fig. 28. Archegonium showing fertilization of the egg-cell.

Fig. 29. Sporangium containing spore-mother-cells; calyptra two-layered.

Fig. 30. Spore-mother-cells becoming rounded off and separated from one another.

Fig. 31. Second division of the mother-cells and young tetrad. Secondary and tertiary thickening layers of the mother-cell wall still surround the periphery of the cells.

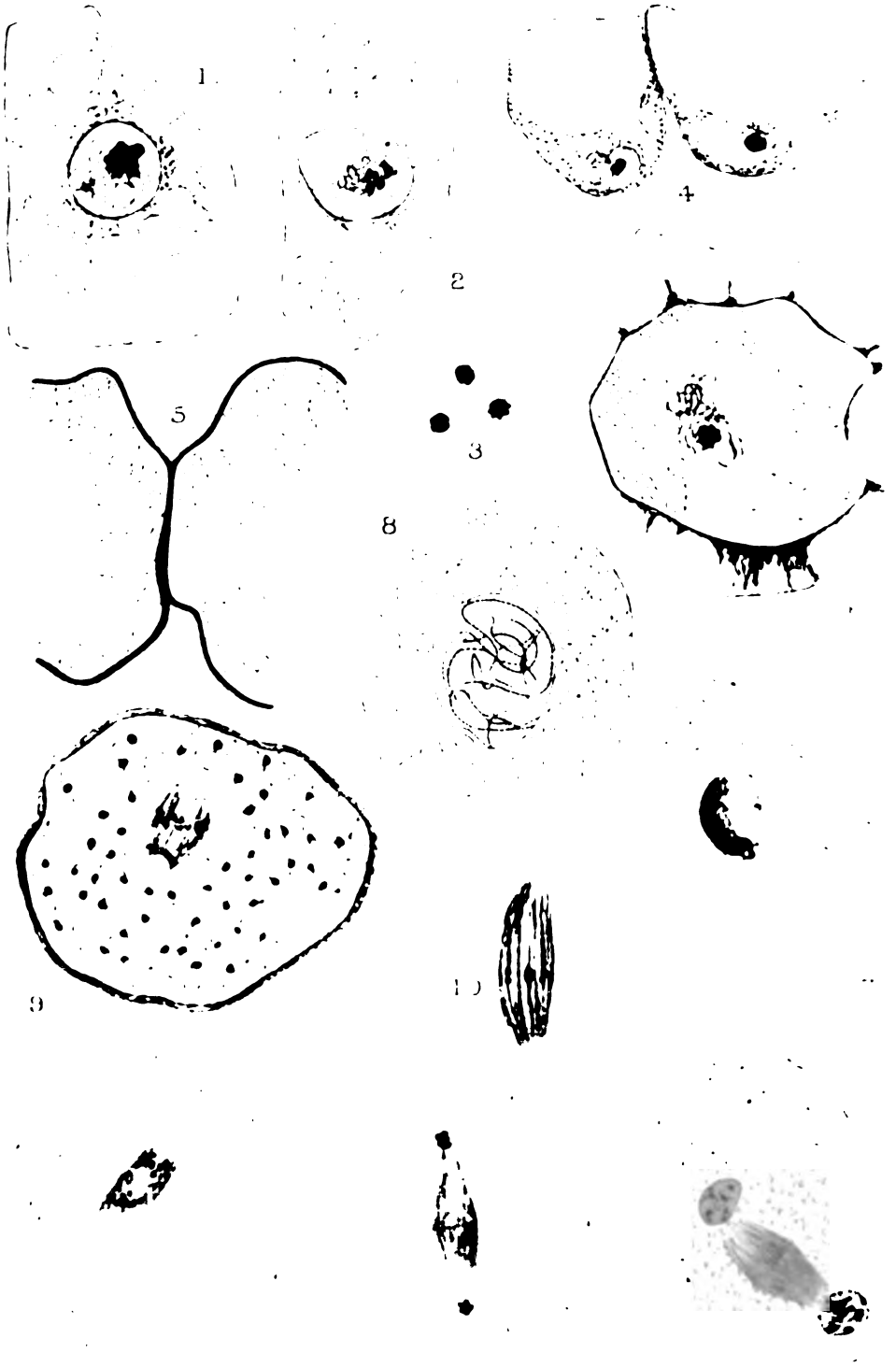
Fig. 32. First division of the egg-cell.

Fig. 33. Sporangium containing spores with two-layered coats. Note mucilage between the spore-tetrads.

Fig. 34. Spore at about middle period of its development treated with iodine solution to show distribution of starch.

Fig. 35. Section of spore showing layers of its wall. Darkly coloured layer is particularly noticeable.

Fig. 36. Section of spores to show the new lamellae which are to be added to the thickness of the second spore-wall plasmolysed away from that wall together with the protoplast to which they are firmly fixed. These lamellae gave cellulose-pectose reactions.



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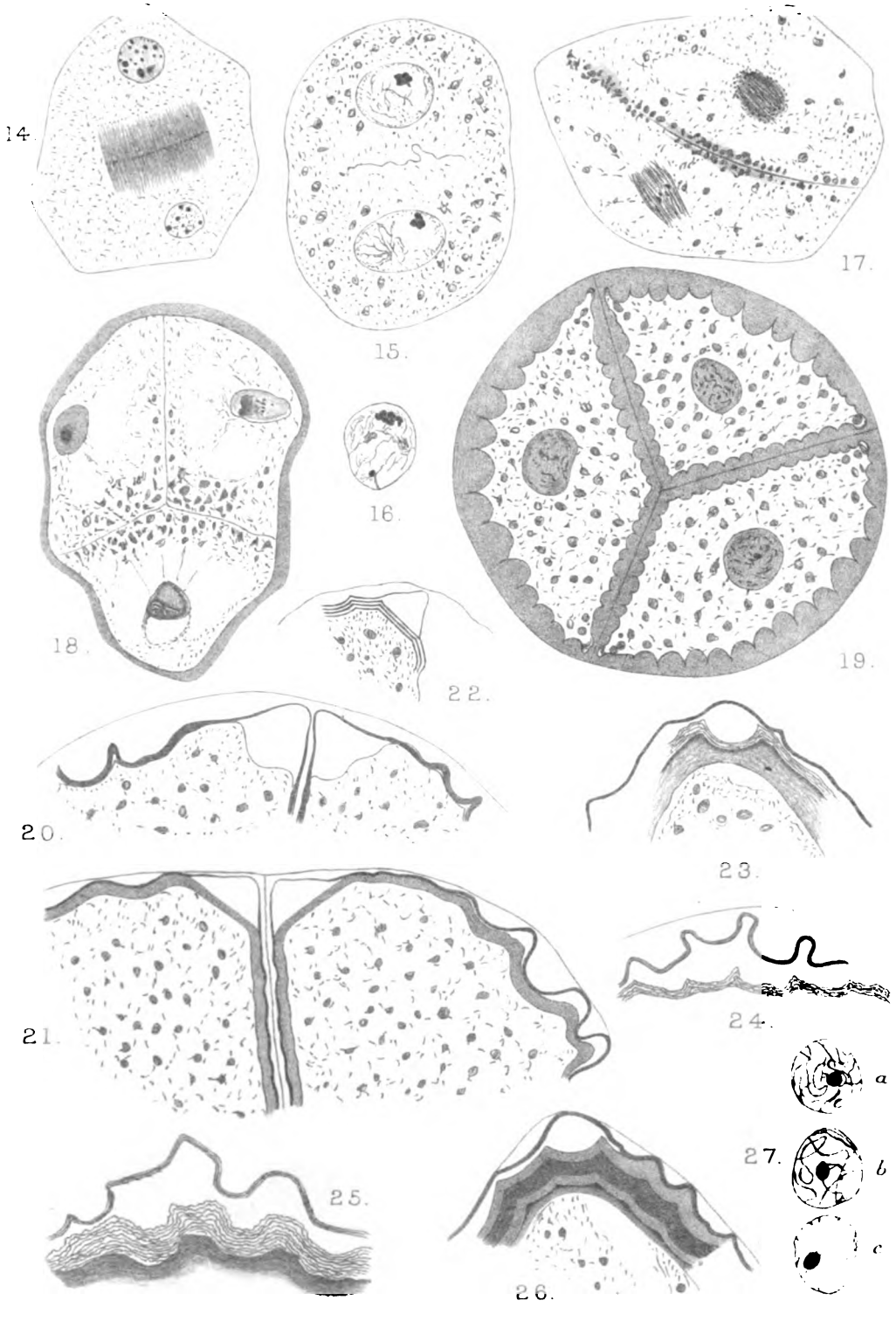
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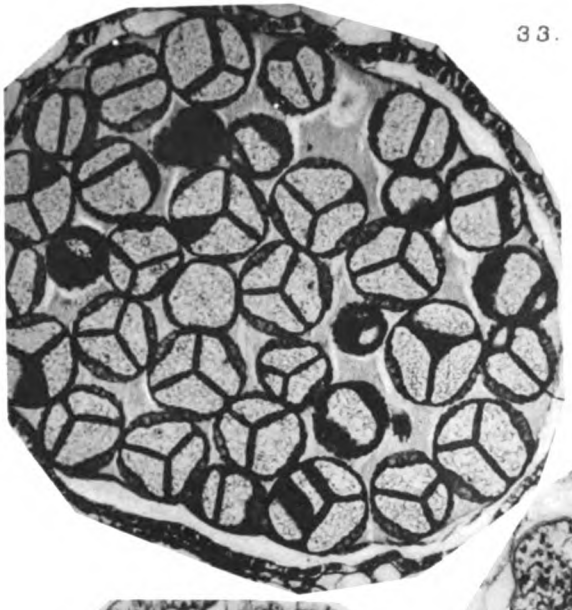

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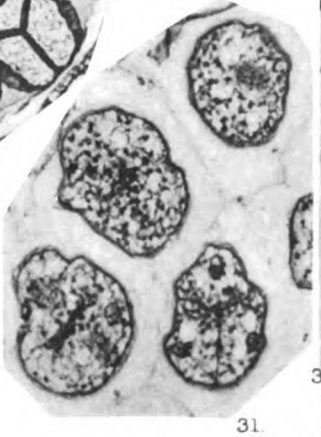

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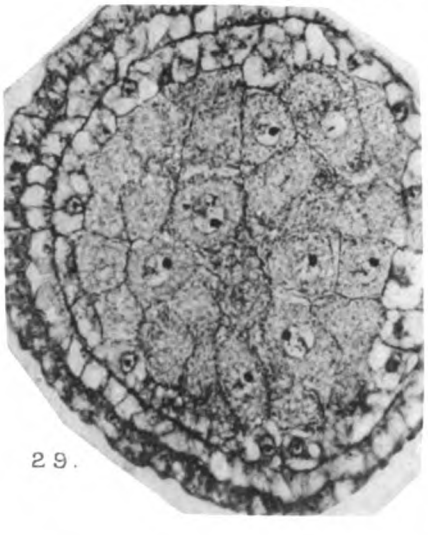

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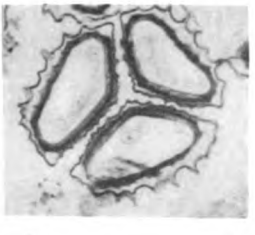

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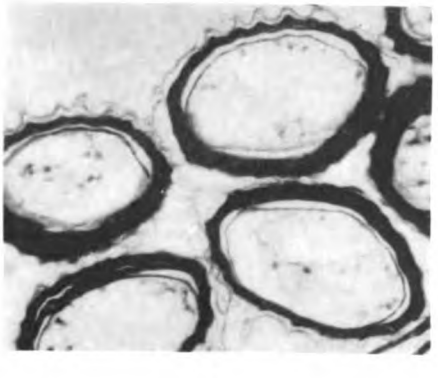

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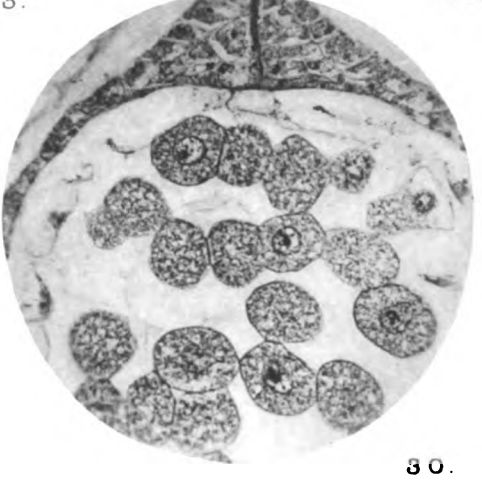

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BEER — RICCIA GLAUCA

The Monoecism of Funaria hygrometrica, Sibth.[1]

BY

L. A. BOODLE, F.L.S.

Assistant, Royal Botanic Gardens, Kew.

With Four Figures in the Text.

THE published statements regarding the distribution of the male and female flowers in *Funaria hygrometrica* are contradictory, this species being described as monoecious in bryological works, while dioecism is attributed to it in various botanical textbooks. In view of the conflicting nature of the different descriptions, Dr. D. H. Scott, F.R.S., suggested to me that I should make an examination of this species, his attention having been drawn to the subject by Prof. Charles Stewart, F.R.S., who informed him that the plant was monoecious.

In the first place a few references to literature may be made. Sachs[2], Van Tieghem[3], and Goebel[4] refer to *Funaria hygrometrica* as an example of a dioecious species, in which the male organs are on smaller plants of shorter duration. Campbell[5] states that '*Funaria* is strictly dioecious,' and adds that the 'male plants either grow separately or more or less mixed with the females.' In agreement with Campbell, Scott[6] describes *Funaria* as dioecious, the male plants as of fair size, and the female plants as very small. Bower and Gwynne-Vaughan[7] describe the sexual organs as occurring on distinct plants. Thus the works quoted above agree as to the dioecious character of the species.

[1] From the Jodrell Laboratory, Royal Botanic Gardens, Kew.

[2] Sachs, Text-Book of Botany, 2nd Eng. ed. (1882), p. 370.

[3] Van Tieghem, Traité de Botanique, 2nd ed. (1891), p. 1350.

[4] Goebel, Outlines of Classification, Eng. ed. (1887), p. 174, and Die Muscineen, Schenk's Handbuch, 2. Bd. (1882), p. 375.

[5] Campbell, Mosses and Ferns, 2nd ed. (1905), p. 195.

[6] Scott, Structural Botany, Part II, 4th ed. (1904), p. 132 et seq.

[7] Bower and Gwynne-Vaughan, Practical Botany for Beginners (1905), p. 211.

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Bruch and Schimper[1] state that the primary stem is terminated by a male flower, and that it subsequently gives rise to fertile [female] branches. Wilson[2] describes the stem as 'at first simple, terminated by a barren [male] discoid flower; subsequently branched, the branches bearing terminal fertile flowers.' Lesquereux and James[3] give the flowers as monoecious and terminal, the male on the primary stems, the fertile on the innovations. Sullivant[4] and Brotherus[5] also describe the male flowers as terminal, and the female as borne on innovations. Limpricht[6] describes *F. hygrometrica* as monoecious, but does not mention the relative position of the male and female organs. According to Braithwaite[7] the plant is autoicous [monoecious], and the male inflorescence terminal on a short basal branch, and Dixon and Jameson's[8] description is similar: (*Funaria*) 'Autoicous in all the British species, male flower discoid, terminal on a lateral branch.' We see then that in all these bryological works *F. hygrometrica* is described as monoecious, though different opinions are given as to whether the male or the female flower is terminal on the primary axis.

As it seemed possible that the divergent statements on the distribution of the sexes might be due to local differences, plants from several localities were examined, but no evidence confirming this view was obtained. The specimens were collected in the following places: Royal Botanic Gardens, Kew, Richmond (Surrey), Seaford (Sussex), Wye (Kent), and near York. The material from York was supplied by the British Botanical Association, Holgate, York, and was accompanied by a letter from Dr. A. H. Burtt, in which the writer mentions that 'of the several thousand hitherto examined during the past few years, by far the larger majority of antheridia-bearing plants had young female branches attached to them. I am indebted to Mr. E. S. Salmon, F.L.S., for the material from Wye.

In a sod of *F. hygrometrica* it is often no easy matter to separate the individual plants, owing to the interwoven growth of the rhizoids borne by the stems. In tearing the rhizoids apart, one is liable to break the connexion between a stem and its branch. Out of 102 specimens I was able to determine that seventy-seven were monoecious, the male and female axes being clearly attached to one another. In sixty-five of these it was evident

[1] Bruch and Schimper, Bryologia europaea, vol. iii (1836–51). *Funaria* is described as agreeing with *Physcomitrium*, in which the position of the male and female flowers is described.

[2] Wilson, Bryologia Britannica (1855), p. 268.

[3] Lesquereux and James, Manual of the Mosses of North America (1884), pp. 200 and 199. Details are given for *Entosthodon*, and *Funaria* is described as similar.

[4] Sullivant, Icones Muscorum (1864), p. 87.

[5] Brotherus, in Engler and Prantl, 1. Teil, 3. Abt. (1903), p. 521.

[6] Limpricht, Die Laubmoose Deutschlands, in Rabenhorst's Kryptogamenflora, vol. iv, 2. Abt. (1895), p. 199.

[7] Braithwaite, The British Moss-Flora, vol. ii (1888–95), p. 136.

[8] Dixon and Jameson, The Student's Handbook of British Mosses, 2nd ed. (1904), p. 300.

at the female axis was a branch of the male. We will return to these ımbers later, after first describing two or three typical specimens.

When a plant, consisting of a male and female axis, has been isolated, is often the case that the rhizoids form such a dense weft on some portions of the stem that the relation of the two axes to one another annot be determined until the greater number of the rhizoids have been issected away. Fig. 1 is a drawing of a plant prepared in this way, several rhizoids being also omitted for the sake of clearness. The long traight stem is the male axis bearing a terminal discoid male flower (♂), n which the antheridia were found to be brown and withered. The branch ın the right ends in the female flower (♀), which contained one nearly

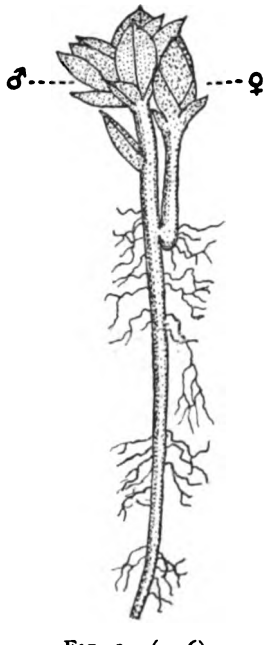

FIG. 1. (× 6).

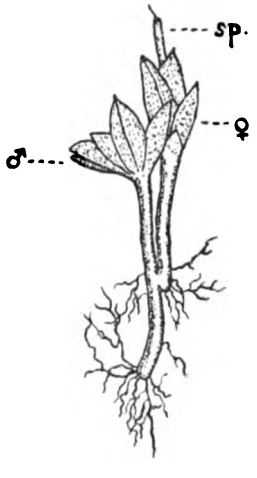

FIG. 2. (× 6).

mature archegonium, as well as two or three others with brown necks. In this specimen it is fairly evident that the female axis has been produced as a branch of the male stem. In many cases, especially in older plants, the main axis may become bent in such a way that the female branch appears at first sight to belong to the primary stem, and the male flower to be on a lateral branch, but the removal of the rhizoids makes the matter clear. The base of the female branch is usually tuberously swollen, and ends in a short free downward prolongation bearing a large number of rhizoids.

A plant somewhat older than the last specimen is shown in Fig. 2. Here the female branch (♀) is inserted at a lower level, and a young

sporogonium (sp.) has been produced by the female flower, the leaves of which now overtop those of the male inflorescence. An older specimen, bearing a nearly mature sporogonium, is shown in Fig. 3, in which the rhizoids have been entirely omitted. The only essential difference from the two preceding cases is that the insertion of the female branch is nearer the base of the male axis.

We have so far relied on the external appearance for determining which is the parent axis, but naturally it was necessary to supplement this by other data. In sections cut through the two axes in the region of attachment, the structure gave evidence of the lateral origin of the female branch. The central conducting strand in the male stem has a straight or even course. That of the female branch, when traced downwards into the tuberous base, comes to consist of several large, and a few small elongated elements, which in the region of attachment run obliquely across towards the central strand of

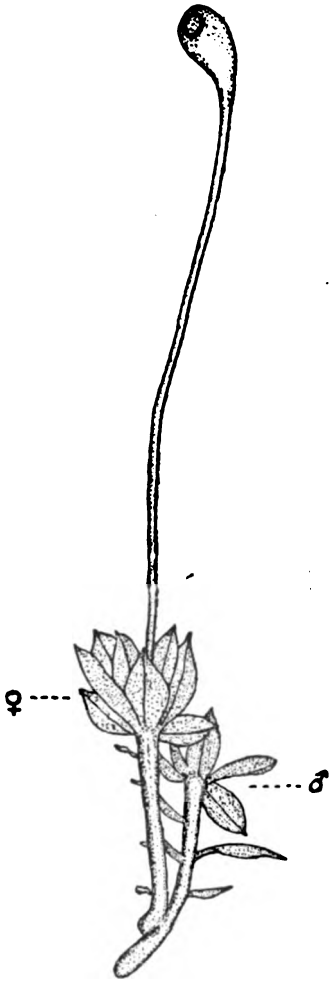

FIG. 3. (× 6).

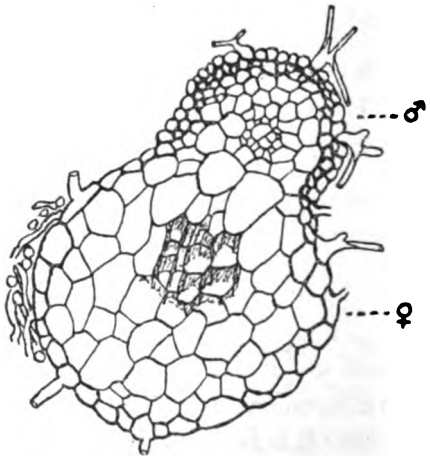

FIG. 4. (× 95).

the male axis, some of the elements terminating nearly, but not quite, in contact with it. A transverse section through the united axes is shown in Fig. 4. The female branch (♀) is considerably the larger of the two, and its central strand is cut obliquely, as it is beginning to curve across towards the male axis. The free base of the female branch consists of large-celled parenchyma, and contains no conducting

tissue. The tissues in the female branch become mature later than those of the male branch at a corresponding level. Further evidence on the same point is given by the fact that male plants bearing young branches (with no sexual organs) were found, but no female plants showing the same character.

To return to the records of the examination of plants; as stated above, seventy-seven specimens out of 102 were proved to be monoecious. We will now inquire into the figures obtained as affecting the proportional number of plants in which the female axis is a branch of the male. This was found to be the case in sixty-five cases. Of the remaining thirty-seven most, at any rate, are not to be regarded as necessarily exceptions to this mode of growth. Firstly, in seven specimens the male and female axes were proved to be attached to one another, but no record was made as to which was the parent stem. This was because, when the first few plants were examined, it was thought that the monoecism or dioecism was the only point in dispute. Next there were five plants in which the two axes were attached to one another quite basally, so that it could not be seen which was the primary stem and which the branch. It may be mentioned here that the level of insertion probably has some relation to the crowding of the moss-plants and the conditions as to dampness. In three cases a male and female axis were closely associated, but attachment was not proved. It is quite likely that the two axes may have been accidentally torn apart in preparing the specimen. Six examples were found of a female branch attached to a stem, on which no sexual organs could be found. In these cases, however, the parent stem showed signs of having been injured at the apex, hence it is quite possible that a male flower may have been present previous to the injury. Four other specimens showed a male stem bearing a lateral branch, on which there were no sexual organs. Judging by the external appearance, these are probably to be interpreted as examples of a female branch borne on a male stem, but too young to show archegonia. Twelve plants remain, viz. three male stems with no branches, and nine female axes apparently unattached. As the female branch develops late, it is possible that the three male plants would have subsequently given rise to female branches.

From what has been said in recording the last thirty-seven cases, it is seen that all except the nine free female plants should be disregarded as clearly inconclusive [1] on the question as to whether female axes are ever produced otherwise than as branches of male stems.

As regards the nine female stems, it may be that they were accidentally detached from male stems in separating them from the sod. When examining the last batch of plants (twenty-two in number) it occurred to me that

[1] The proportional number of inconclusive specimens would have been greater if tufts had been specially chosen in which basal attachment was common or young male plants numerous.

by cutting sections of any apparently free female stems it might be possible to obtain evidence of previous attachment to another axis, if the female stem had been formed as a branch. Among this series only one independent female stem was found, and this certainly had a scar in its basal region suggesting a broken attachment. Hence the nine apparently free female stems all come under suspicion, especially as most of them were among the earlier plants examined, when less care was taken in separating the specimens; consequently one may say that the female axis is produced as a branch of the male in the majority of cases, perhaps in all.

No certain case was observed of a female stem producing a male branch. Male plants remaining unbranched may perhaps occur, but as far as these observations go they must be relatively rare.

We have restricted our view to the relation of the female branch to the male stem bearing it, but branching may be carried further. Thus a plant was observed in which the male axis had given off a male branch, which in its turn had produced a female branch. A few other specimens were probably similar, but the primary axis was partly decayed, so that the presence of antheridia on it could not be determined. Evidence of branching carried to a higher order was obtained, and one or two cases of the production of more than one branch on a single male axis were also seen.

We may observe that the production of the female axis as a branch, of rather late origin, on the male stem appears often to lead to the maturing of the archegonia at a time when the antheridia of the same plant are empty and withered, so that cross-fertilization occurs.

One phaenological record regarding *F. hygrometrica* made by Grimme[1] in Germany may be quoted as agreeing well with the formation of the female axis as a branch of the male: 'numerous male flowers with almost mature, yellowish-brown (and also green) antheridia. One female inflorescence with immature archegonia.'

The result of the present observations is to confirm the statements of Bruch and Schimper, Wilson and other bryologists, and agrees with the observations of Dr. A. H. Burtt. The distinct contrary statements made in different textbooks are at first sight difficult to understand, but the explanation is probably as follows. In certain cases numbers of distinct male plants can no doubt be found, most, if not all of these being young specimens which have not yet produced female branches. This gives a first impression of dioecism. Again, when obtaining a specimen for examination, if one pulls a female branch on the edge of a tuft of plants, it will often come away, leaving the primary male axis behind. If greater care be exercised and a clump of two or three plants be put on a glass slide for separation under a dissecting microscope, the slight difficulty in tearing apart a male and female axis may easily be attributed to the

[1] Grimme, Ueber die Blüthezeit deutscher Laubmoose, &c., Hedwigia, 1903, p. 38.

resistance of the rhizoids, which invest the region of attachment. In both cases, when the female branch has been separated, it appears like an independent plant on account of its rounded base (which bears a tuft of rhizoids), the scar being lateral, above the base, and hidden by rhizoids. Also, when the female plant is old, the male stem sometimes begins to decay away, and it is probable that from this cause actually free female branches may be found. The statement of Sachs, Goebel and Van Tieghem, that the male organs are on smaller plants of shorter duration, probably refers to this and to the fact that the female branches in most cases ultimately overtop the male. Campbell [1] states that the male plants are about one cm. in height, but that the archegonia are formed while the female plant is still very small—a few millimeters in height. Substituting 'axis' for 'plant,' this is true especially in those cases in which the female branch is inserted near the top of the male stem (see Fig. 1 of the present paper).

Summary.

Funaria hygrometrica is as a rule monoecious, and, where the point could be determined, the female stem was a branch of the male. The male axis bears a terminal male flower, and produces a lateral branch (innovation), which forms a terminal female flower. The female branch may be inserted at different levels, sometimes high up, sometimes basally; it usually has a tuberous base bearing a tuft of rhizoids, and, if torn away, appears like an independent plant. In the region of attachment the conducting strand of the female branch terminates nearly in contact with that of the male stem. The male axis bearing the female branch may, in its turn, be a branch of another male stem. Dioecism, if it occurs, is comparatively rare.

Addendum.—I am indebted to Mr. H. N. Dixon, F.L.S., for a further supply of *Funaria hygrometrica*, which he kindly collected for me at Collyweston, Northants. The material was from an oolitic limestone-quarry. The rhizoids were numerous, and held a large amount of fine limestone soil, hence examination of the specimens was difficult.

Twenty plants examined included: fourteen in which the female axis was clearly a branch of the male stem; four in which the two axes were attached to one another basally; one female branch attached to a decayed stem; and one female axis apparently unattached. Thus the results obtained are confirmatory of those given above. Some of this material showed rather prolific branching, similar to that described on p. 298.

[1] Campbell, loc. cit.

The Statices of the Canaries of the Subsection Nobiles. II.

BY

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With a Map in the Text.

IN the first part of this paper (pp. 206–12 of the present volume) I have discussed the history and distribution of *Statice arborea*. I propose now to deal in a similar way with the other Statices of the *Nobiles* group and sum up their principal characters in a sort of expanded key, reserving the description of the hybrids and a paragraph of a more general character for a third and concluding part.

STATICE MACROPHYLLA.

This has already been mentioned in the first part of my paper. It is a very distinct and, apart from the variety (?) *sinuata* to which I refer later on, perfectly homogeneous species. Unlike *Statice arborea* it is still flourishing, although confined to a narrow belt on the north-east coast of the island. It was discovered by Broussonet, who is probably the author of the name *Statice macrophylla*, although he never published it. The first description, a very short diagnosis, was by Sprengel[1] in 1825. He, however, attributed the name to Willdenow and not to Broussonet, as is usually quoted. On the other hand, Steudel[2] coupled it with Link's name; but neither Willdenow nor Link published anything on the subject. Broussonet's specimens of *Statice macrophylla* which were in the Montpellier herbarium have been lost. Boissier seems to have seen them, or at least some duplicates distributed by Broussonet, as he quotes them in his monograph of the Plumbagineae, confining himself, however, to the note 'In Teneriffâ, Brouss.[3]' Fortunately an important record concerning them is preserved in F. de Girard's manuscript of a memoir on *Statice* which was never

[1] Sprengel, Systema Vegetabilium, i, p. 959. [2] Steudel, Nomenclator Botanicus, ed. II, p. 633.
[3] Boissier in De Candolle, Prodromus Systematis Naturalis Regni Vegetabilis, xii (1848), p. 637.

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published, having been forestalled by Boissier's monograph of the Plumbagineae. The manuscript is at present in the Institut Botanique of Montpellier, and Mr. R. N. Rudmose Brown has been good enough to copy for me the passage in question. It runs thus:—'Hab. (viz. *Statice macrophylla*) Teneriffe, loco dicto la Puenta de Teno nec non Passo de la Cueva legebat olim Broussonetus.' Punta de Teno is the westernmost point of the island, close to El Freyle where the stunted form of *Statice arborea* (pp. 208 and 212) still occurs. The other locality I could not trace exactly; but I assume it is a place not far to the east of Cape Hidalgo and above Cueva de Pope, a locality marked in Webb's map of Teneriffe. If this is correct, Paso de la Cueva comes within the area where *Statice macrophylla* has been observed in more recent times. This is a small belt of rocky coast-land, extending from somewhere near Punta del Viento towards Taganana, and skirting the northern slopes of the Anaga Hills. The first after Broussonet to collect it there were Webb and Berthelot, who in 1828 or 1829 found it 'in montosis herbidis Teneriffae ad vallem de la Goleta et ad montem Bajamar[1].' According to Webb's map La Goleta is a small valley extending 3 or 4 km. inland, from a point a little to the east of Punta del Viento, and west of the Mesa de Tejina. L. von Buch has it farther east, and Bolle's[2] description would also seem to place it east of the Mesa de Tejina and immediately at the western end of the cliffs of the Costa de Bajamar which trends towards Punta del Hidalgo. Possibly Webb's indication of locality refers to one place only, and should read 'La Goleta, ad montem Bajamar' as indeed Bourgeau, who collected the plant in the same place in 1846, puts it in his label ('in rupestribus herbosis vallis de la Goleta, Bajamar'). Perraudière found it nine years later (March 29, 1855) 'in collibus ad marginem sylvarum Anaga.' This is somewhat vague; but as Perraudière collected on the 20th of the same month in 'Anaga. reg. bor. mediâ,' it is practically certain that he meant the northern slopes of the Anaga Hills. Here, east of Punta del Hidalgo, it was observed by Dr. Cabrera (as the Rev. R. P. Murray informs me) near Taborno among rocks in 1901, and according to a note from Dr. Perez, which I owe to the courtesy of the same gentleman, it occurs plentifully in the valley of Afur, at a spot called 'El Tablero,' a sort of headland above the sea, and about 2·5 km. to the west of Taganana. Taking Punta del Viento as the western and El Tablero as the eastern end of this area, its length would be about 25 km. To this would, however, as Dr. Perez has just informed me, have to be added an outlying and hitherto unknown station on the high cliffs below the 'Calvary' of Santa Ursula, 5 km. to the north-east of the town

[1] Webb et Berthelot, Histoire naturelle des Iles Canaries, III, iii, p. 180. See also their Atlas, tab. ii and iii.

[2] Bolle in Zeitschrift für allgemeine Erdkunde, vol. xl (1861), p. 89.

of Orotava, whilst in Broussonet's locality at Cape Teno we have an indication of a western area where *Statice macrophylla* has become extinct within the last hundred years.

As to Mann's La Longuera station I have made some suggestions on p. 211. Dr. Perez has since written that he still thinks Mann meant La Longuera on the Burgado Cove where he also gathered *Statice arborea*. From Dr. Perez's remarks it would, however, appear that *Statice arborea* was not wild there, but grown by a peasant near his cottage, and this may also have been the case with Mann's *Statice macrophylla*.

I have mentioned above a 'variety (?) *sinuata*' of *Statice macrophylla*. It was described by Boissier[1] from a specimen received in 1846 by Bourgeau from S. Isidro in Gran Canaria. Through the courtesy of Mr. W. Barbey I have been able to examine the type of this variety. It exactly matches the Teneriffe specimens of *Statice macrophylla* with the exception of the wider and undulate axial wings. Bourgeau on his label says 'Je ne sais pas s'il est cultivé.' Now, there is in the Kew Herbarium a typical specimen of *Statice macrophylla* gathered nine years earlier by Kirkman Finlay (a correspondent of Sir William Hooker) in 'Mr. Duthie's grounds' in Gran Canaria. This I take to be from a cultivated plant, and so was in all probability Bourgeau's.

The date of introduction of *Statice macrophylla* into English horticulture is given as 1824 by Loudon[2], and the introduction itself is credited to 'Mr. Smith of the Botanic Gardens of Hull' by Sir William Hooker[3]. It seems to have gone out of cultivation long ago, or has, at any rate, become very rare.

STATICE IMBRICATA.

If *Statice arborea* exists at present only in a stunted form in the extreme west of Teneriffe, and *Statice macrophylla* is confined to a narrow belt on the north-east coast, *Statice imbricata* occupies geographically an intermediate position. It was discovered by Broussonet on El Roque de Garachico, a rock in the sea opposite to the town of Garachico. Here Webb found it again about thirty years later, but it was not made known until 1844 when F. de Girard[4] described it, taking up Webb's manuscript name. Webb and Berthelot[5] also observed it 'capris tonsam' on a spot between the Villa Fuente del Cuerbo and the sea, two kilometres to the north-west of the town of Buena Vista. It still was there or in the immediate neighbourhood on sea cliffs in 1855, when Perraudière collected it. A third locality was discovered by Bourgeau in 1846, a few kilometres east of

[1] Boissier, l. c. p. 637.
[2] Loudon, Hortus Britannicus (ed. 1830), p. 115.
[3] W. Hooker in Botanical Magazine, tab. 4125 (1844).
[4] Girard in Annales des Sciences Naturelles, 3me série, ii (1844), p. 330.
[5] Webb and Berthelot, l. c. III, iii, p. 179.

Tacoronte and known as La Hondura. Here, too, it grew on sea cliffs. La Hondura is some kilometres to the west of the valley of La Goleta as marked in Webb's map, and therefore near the western end of the area of *Statice macrophylla*. The three little areas inhabited at present by *Statice imbricata* are therefore from west to east: (1) The sea cliffs of Buena Vista, about 7–8 km. east of Punta de Teno; (2) El Roque de Garachico, about 8–9 km. farther east, and (3) La Hondura near Taraconte, about 30 km. east of Garachico.

Statice imbricata is little known in cultivation. From notes by Don[1] and Nicholson[2] it would appear that it was introduced by Webb in 1829; but in 1848 it was spoken of and figured in Flore des Serres[3] as a new introduction, and it was stated that the plants were raised from seeds sent to Europe in 1846 by Webb's collector, which evidently means Bourgeau.

STATICE BRASSICIFOLIA.

In 1845 Bourgeau discovered two Statices in the islands of Gomera and Hierro respectively, which were described by Webb[4] as *Statice brassicaefolia* (sic) and *Statice macroptera*. He admitted, however, their great similarity and left it to future explorers to examine whether they were not forms of one species. I may remark at once that specimens collected since then leave no doubt that the plants which Webb described as *Statice brassicifolia* and *Statice macroptera* were merely slight variations of what most botanists would consider as one species, differing in stature, pubescence, and width of the axial wings and the subfloral auricles. This view is supported by Perraudière's discovery (1855) of *Statice brassicifolia* in the *locus classicus* of *Statice macroptera*. The differences should, however, not be entirely disregarded, as they seem to be constant, at least within certain limits. Thus specimens raised at Kew from seeds gathered by Bourgeau in Gomera, the *locus classicus* of *Statice brassicifolia*, preserved the general facies of that form, which in contradistinction from *Statice macroptera* is determined mainly by narrower axial wings and subfloral auricles, and by slightly denser pubescence. One of the Kew specimens was figured in the Botanical Magazine (tab. 5162) in 1860—that is fifteen years after Bourgeau's discovery—and the figure agrees entirely with Webb's plate of *Statice brassicifolia*. On the other hand, there is a specimen in the Temperate House at Kew, labelled '*Statice brassicifolia*, garden origin,' which combines the wider, deeply-lobed wings of *Statice macroptera* with the smaller and more pubescent auricles of *Statice brassicifolia*. This specimen, the history of which I have not been able to trace, may be a descendant of the Gomera

[1] Don, Hortus Cantabrigiensis, 13th ed. (1845), p. 187.
[2] Nicholson, Dictionary of Gardening, iii. p. 492.
[3] Flore des Serres, iv (1848), Pl. 320–321.
[4] Webb and Berthelot, l. c., III, iii, pp. 181, 182.

plant, figured in 1860. In those circumstances it will be best to distinguish the two extreme forms as *Statice brassicifolia* (typica) and *Statice brassicifolia*, forma *macroptera*. Neither has been found anywhere outside the islands mentioned, and even there they are confined to a single station in each, namely in Hierro to some steep rocks above Savinosa, on the crater bay of El Golfo on the north side of the island (both forms), and in Gomera to some grassy ledges high up on the gigantic cliff, known as El Risco de las Sulas near Agulo (only the typical form). The Rev. R. P. Murray collected both forms as late as 1899, and each in its *locus classicus*.

I have already referred to the introduction of *Statice brassicifolia* (typica). The form *macroptera* was raised by Messrs. Thibaut and Keteleer of Paris, presumably from seeds gathered by Bourgeau in 1845, and a fine specimen of theirs was figured in Illustration Horticole (Pl. 105) in 1856. Both are, however, now very rare in cultivation.

STATICE PUBERULA.

We have seen that in *Statice arborea* and *Statice brassicifolia*, there is a range of variation great enough to have suggested the presence of distinct species. In *Statice puberula* this range is still greater, and affects all parts with the exception of the 'spicae' and the ultimate divisions of the inflorescence, both being remarkably uniform throughout. *Statice puberula* was discovered by Webb and Berthelot[1] in 1829. They found it in the island of Lanzarote on the western precipices of the Famara, a basaltic range overhanging the narrow straits of El Rio, which separate Lanzarote from the small island of Graciosa, and also on the other side of El Rio in Graciosa itself. Webb sent seeds of it to his home-place at Godalming, and a plant raised from them was described and figured as *Statice puberula*, Webb by Lindley[2] in 1831. Webb's specimens represent an extremely stunted form, scarcely 1 dm. high, with inflorescences about 4 cm. (or less) across, and dense rosettes of small leaves, the longest blades not much exceeding 3 cm. The leaves are, like the primary axis of the inflorescence, loosely covered with coarse stellate hairs and entire, without a trace of lobing in the decurrent bases. The cultivated specimen figured by Lindley was about twice as high and had a much looser inflorescence, almost 12 cm. across, wingless peduncles, and entire leaf-blades up to 6 cm. long. Another figure of a cultivated specimen of *Statice puberula*, no doubt of the same origin, and published in the Botanical Magazine (tab. 3701) in 1839, represents a plant almost 3 dm. high, with an inflorescence of about the same size as in Lindley's plant, but with its primary branches narrowly winged. The blades are up to 4 cm., and the slender petioles up to 6 cm.

[1] Webb and Berthelot, l. c., III, pp. 27, 28, and III, ii, p. 178.
[2] Lindley in Botanical Register, tab. 1450.

long, and in some of the blades there is an indication of lobing. A specimen cut from a plant in cultivation at Kew in Sir William Hooker's time is almost a complete match of the figure in the Botanical Magazine, which was drawn from a plant grown in Edinburgh. Another specimen from a plant at Kew, but of recent cultivation is also very similar to the latter, but the lobing of the blade is more pronounced and extends to the decurrent base, and I might add, the blades are somewhat larger (up to 5 by 3 cm.). This deviation from the original type when under cultivation has a complete parallel in a specimen collected by Lowe (in 1858) on the 'cliff above the Salinas, Haria,' which is evidently the same locality as Webb's and Berthelot's on the Famara, the Salinas being situated on El Rio, close under the cliffs of the Famara. One of the leaves shows distinct lobing at the base, and one or the other of the primary branches of the panicle is narrowly winged. On the other hand, Low also collected with it a barren rosette agreeing exactly with Webb's originals from Graciosa. This marks, so far as we can safely say at present, the range of variation such as may be considered as the direct result of external conditions, and it was necessary to mention those details in order to appreciate the position of another form from the same locality, and generally admitted as a distinct species, viz. *Statice Bourgaei*. Its history is briefly this. In 1845 Bourgeau collected in the island of Lanzarote, in a place 'Los tanques de Famara,' a plant which he distributed as *Statice puberula* (No. 335). In the following year he issued it again (No. 564), but this time as *Statice Bourgeaei* (sic), Webb, and with the indication 'in rupestribus Famara.' The two plants are absolutely identical, and differ from the original *Statice puberula* in being 4–5 dm. high, and correspondingly more robust, and in having very much larger leaves, the blades measuring up to 10 cm. by 8 cm., and varying from ovate to suborbicular or elliptic-oblong with a suddenly contracted, decurrent, and usually sinuately-lobed base. The primary axis, and some of the primary branches of the inflorescence, are narrowly and unequally winged. The indumentum is of the same nature as in Webb's *Statice puberula*, and the flowers also agree perfectly with those of that plant. Boissier gave a full description of *Statice Bourgaei*, Webb, in 1848[1], based on Bourgeau's No. 564, whilst he refers, curiously enough, No. 335 to *Statice puberula*. He describes the leaves much as I have done in the preceding lines, and adds that the flowers are twice as large as those of *Statice puberula*. Neither this statement nor the indication of certain minor differences in the characters of the bracts are borne out by the material at my disposal. *Statice Bourgaei* was raised at Kew from seeds communicated by Bourgeau. It flowered here for the first time in 1859. A specimen cut from it in 1861 might be described as a reduced and glabrescent edition of Bourgeau's No. 564, the largest blade measuring only 10 by 5 cm. To judge, however,

[1] Boissier, l. c., p. 638.

from the figure published in Flore de Serres (tab. 2292) in 1877, and drawn from a plant received from Kew, the Kew stock of *Statice Bourgaei* attained subsequently quite the dimensions of Bourgeau's herbarium specimens distributed under No. 564, and the same may be said of a plant still in cultivation at Kew.

During the last few years Kew received from Dr. Perez a fine suite of specimens which were put down either as *Statice Bourgaei* or as nearly related to it. They may be grouped in four sets.

Set 1 marked '*Statice Bourgaei* (original plant from Famara)' agrees with Bourgeau's Nos. 335 and 564, except in so far as the specimens are still more robust, and have all the leaves broad-ovate with a suddenly contracted, decurrent, and mostly (not always) lobed base, the blades measuring up to 13 by 10 cm., excluding the decurrent base.

Set 2 represents a plant which—if I interpret Dr. Perez's note correctly—was originally received from Lanzarote, and had been in cultivation with Dr. Perez for how long I cannot say, but apparently not for more than one or two years. The specimens of this set have much enlarged inflorescences, up to 25 cm. high (from the lowest branch) and as broad, with more conspicuous but irregular wings, and less hairy almost orbicular blades (about 10–11 cm. in diameter), and with more or less decurrent and usually sinuately-lobed bases.

Set 3 was raised from seeds received from Ye, a locality, according to Dr. Perez's description, evidently not very far from the Salinas, and half an hour from the seashore. The blades are still more glabrescent than in set 2, have entire decurrent bases, and also show in their upper parts only traces of lobing, or even not as much as that, whilst the wings of the primary axis of the inflorescence vary from 1·5–13 mm. in width.

Set 4 has magnificent large inflorescences and leaves like those of set 2, but quite glabrous, and axial wings varying from 2–8 mm. width. It originated from seeds, also gathered in Lanzarote, but where is not stated.

In spite of the considerable diversity exhibited by the plants of Dr. Perez's four sets, I do not hesitate to consider them merely as individual variations of *Statice Bourgaei*, some characters of which have probably become particularly accentuated under the influence of cultivation.

I have already pointed out that Webb and Berthelot's and Lowe's stations of the typical *Statice puberula* are identical, and they cover evidently a very small area. 'Los Tanques' I have not found in any map, but it is very likely in the neighbourhood of the Salinas. In any case it is in the Famara, and I believe I am right in tracing all the plants of Dr. Perez's four sets to the same district, so that the area inhabited by *Statice puberula* and *Statice Bourgaei* covers a small piece of rocky coast on the south side of El Rio, whilst an equally small or still smaller strip of land on the northern side of El Rio harbours exclusively the dwarf *Statice puberula*.

We find then here in the north of Lanzarote, and in the adjoining Graciosa, within a very small area—it might be almost said in the same locality—two types of a *Statice*, indistinguishable in their floral characters, and also connected with each other (and at the same time distinguished from all their allies of the *Nobiles* group) by the nature of their indumentum, but otherwise fairly well marked. They each have its own range of variation, though on parallel lines, and they are both plastic to a certain degree. Considering all that, it seems to stand to reason to treat them as varieties of one species. For this the name *Statice puberula* would have to stand, whilst the varieties might be distinguished as var. *typica* and var. *Bourgaei*. The differentiation of *Statice puberula* into two forms is comparable to that of *Statice arborea* and *Statice brassicifolia*, but much more pronounced. This I have indicated by introducing the term 'variety' instead of 'form' into the names. Whilst in the case of *Statice arborea* and *Statice brassicifolia* it is impossible to say which of the two forms in each case is the older, it seems to be quite evident that *Statice puberula* var. *Bourgaei* approaches much more closely its allies of the *Nobiles* section than *Statice puberula* var. *typica*, which betrays in every one of its vegetative characters its specialization in the direction of adaptation to the conditions of an excessively arid region. There is, as far as I am aware, no record of a former extension of the area of *Statice puberula*, but there can be no doubt that its present stations on El Rio are only the remnant of a much larger area.

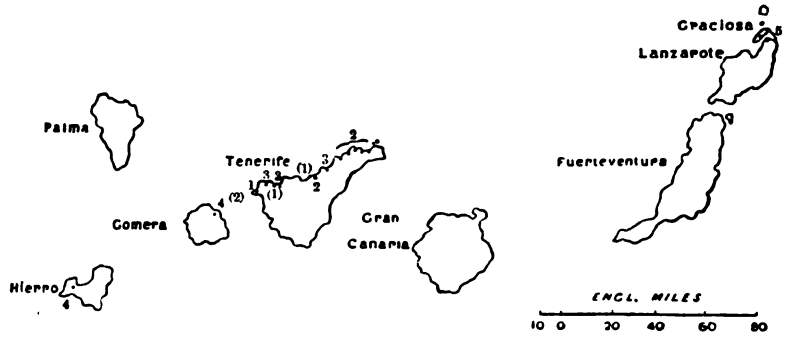
Statice preauxii.

Under this name Webb[1] described a species, specimens of which had been sent by Despréaux from Gran Canaria ('a Canariâ misit'). Boissier[2] puts it more definitely, so as to imply that it was a native of Gran Canaria ('In insula Canariâ. Despréaux!') According to Lasègue[3], Dr. J. M. Despréaux resided for a considerable time in Gran Canaria, but in 1835 also visited Teneriffe, Fuerteventura, Lanzarote, Hierro, and Gomera. But there is some uncertainty about the exact origin of Despréaux's Canarian plants, and Webb[4] denies that he ever was in Hierro and Gomera, although he may have received plants from there. It may well be that he sent the original specimens of *Statice Preauxii* from Gran Canaria, but had originally obtained them from somewhere else. In any case it has not been observed by any one else in Gran Canaria. Webb compares it with *Statice arborea*, Boissier places it with *Statice puberula* and his *Statice Bourgaei*. I have not seen it, but excepting that the leaves are said to be very coriaceous and compared by Boissier to those of *Aegialitis*, there is nothing in the description either of Webb or of Boissier to separate it from the polymorphous *Statice*

[1] Webb and Berthelot, l. c., III, iii, p. 181. [2] Boissier, l. c., p. 638.
[3] Lasègue, Musée Botanique de M. R. Delessert, p. 187.
[4] Webb and Berthelot, l. c., III, iii, p. 182, footnote.

puberula (sensu latiore). In the circumstances, however, I prefer to leave open the question as to origin and position of this species.

I insert here a sketch-map of the Canarian Archipelago, which may serve as a summary of our present knowledge of the distribution of the Statices of the *Nobiles* group.



Distribution of the Statices of the *Nobiles* group—
1. *Statice arborea.* 2. *Statice macrophylla.* 3. *Statice imbricata.*
4. *Statice brassicifolia.* 5. *Statice puberula.*
The figures in brackets mark stations from which the species has disappeared in recent times.

As there exist excellent figures and fairly good descriptions of all the species mentioned above (with the exception of the dubious *Statice Preauxii*), I do not consider it necessary to describe them over again *in extenso*; but I thought it might be useful to add short diagnoses put together in the form of a key, a sort of condensed *descriptions fractionnées et classées*[1]. They would bring out the salient characters of the species, and at the same time facilitate identification.

KEY.

Ultimate divisions of the panicle winged, with the wings widened upwards and produced into auricles; pubescence, if any, uniform.

Glabrous or nearly so (only the ultimate or subultimate divisions of the panicle sometimes sparingly pubescent); primary axis of the inflorescence and its primary divisions wingless or very narrowly winged; auricles below the 'spicae' usually produced into fine, often sickle-shaped points; inner bracts with distinct laterally-compressed, abruptly-ending keel and narrow scarious margin; leaves distinctly petioled, blades often slightly undulate and shallowly sinuate at the decurrent base.

Bare main stem several feet high; leaves to over 30 cm. by 13 cm. **S. arborea (typica).**

Bare main stem very short, branches from the ground or almost so; leaves rarely over 10 cm. by 5 cm. **S. arborea f. frutescens.**

[1] De Candolle, Phytographie, p. 68.

Pubescence extending over the whole plant, or confined to the ultimate divisions of the panicle and the bracts; primary axis of the inflorescence and its primary divisions winged; auricles below the 'spicae' obtuse, rarely with a short broad acute point; inner bracts rounded on the back, and with a conspicuous crisp blue frill; leaves sessile or petioled, blades entire or sinuately lobed.

Only the ultimate and subultimate divisions of the panicle and the bracts pubescent; axial wings narrow; leaves sessile, entire, long attenuated towards the base. **S. macrophylla.**

All over pubescent, when young, or permanently; axial wings broad; leaves petioled, lobed.

Pubescence delicate; auricles below the 'spicae' broad; leaf-blades deeply sinuately lobed below the middle.

Pubescence more or less persistent; axial wings up to 13 mm. broad; auricles below the 'spicae' up to 4 mm. broad. **S. brassicifolia (typica).**

Pubescence gradually more or less disappearing; axial wings up to 25 mm. broad; auricles below the 'spicae' up to 9 mm. broad. **S. brassicifolia f. macroptera.**

Pubescence dense, velvety, persistent; auricles below the 'spicae' small; leaf-blades runcinately pinnatipartite, lobes obovate to obliquely reniform, overlapping, decreasing basewards. **S. imbricata.**

Ultimate divisions of the panicle not winged or auricled; leaves with coarse, stellate or fascicled hairs, rarely glabrous; inflorescence uniformly pubescent in the upper part, with intermixed coarse fascicled hairs on the primary axis and main branches.

With the small inflorescences up to 1 dm. high; leaf-blades in dense rosettes up to 3 (rarely to 6) cm. long, not, or very obscurely, lobed. **S. puberula (typica).**

With the large inflorescences up to 5 dm. high; leaf-blades in loose rosettes, up to 11 cm. long, the decurrent base usually lobed. **S. puberula var. Bourgaei.**

Fruit-dispersal in Adenostemma viscosum[1].

A Biological Study.

BY

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With Plate XXIII.

IN the flower-like inflorescence of the Compositae, as is well known, the usual protective function of the calyx is performed by the involucre. This being so, the calyx proper is either very much reduced (in a few instances entirely suppressed), or else it becomes a highly modified 'pappus,' which appears to be, in a great number of cases, specially adapted to facilitate fruit dispersal. The pappus may assume a variety of forms, such as the well-known parachute mechanisms of many species, the hooked bristles of *Bidens*, etc., etc. But amongst this aggressive and dominant family, the genus *Adenostemma* appears to be unique in one particular, i. e. the possession of a sticky, glandular pappus[2].

It has been noted by more than one writer, that this peculiarity aids the plant in the dispersal of its fruits. Trimen states that the achenes of *Adenostemma* adhere to surrounding objects by their very viscid stalked glands (pappus)[3]; while Hildebrand points out that in its sticky pappus the plant possesses an excellent means of fruit-distribution by the agency of animals. Fritz Müller sent him some seeds of *Adenostemma*, which unfortunately did not germinate, and so, said he, 'it was impossible to study this interesting example any further[4].' As the whole mechanism of dispersal in this plant forms a good example of co-ordinated adaptation, it may perhaps be worth describing in some detail.

[1] See the abstract of a paper read by the author before Section K of the British Association. B. A. Report, Southport, 1903, p. 859.

[2] The generic name, indeed, has reference to this fact—ἀδήν, a gland, and στέμμα, a crown: see Forster, Characteres Generum Plantarum, London, 1776, p. 90.

[3] Trimen, a Handbook to the Flora of Ceylon, London, 1895, vol. iii, p. 13.

[4] Hildebrand, Ueber die Verbreitungsmittel der Compositenfrüchte, Bot. Zeitung, 1872, vol. xxx, p. 12.

[Annals of Botany, Vol. XX. No. LXXIX. July, 1906.]

My own attention was first called to this method of fruit-dispersal in *Adenostemma viscosum*, Forst., during a visit to the Malay Peninsula [1] in the year 1899, by finding one day a few of its fruits firmly gummed to my legs, by means of some short, sticky processes. The latter are in reality the glandular setae (generally three in number) which in this plant represent the pappus. These setae, or stalked glands, are situated on a projecting ring of tissue (the calyx ring), which crowns the inferior ovary (Fig. 4). At the base of each seta is a swelling, which is visible only during the flowering stage (*p.* Fig. 4).

As in the capitula of many other Compositae, the torus, during the ripening of the fruits, assumes a more convex shape, while the involucral bracts, which are at first erect, become spreading, and finally completely reflexed (Figs. 1–3). Meanwhile, all the corollas of the capitulum, as well as the styles, are detached at their bases, and fall off *en masse* (Fig. 2). The pappus now begins (usually, in the cases observed, before the actual throwing off of the corollas) to excrete an exceedingly viscid, clear liquid, which forms a large drop surrounding the tip of each seta. In this condition the pappus setae bear a marked resemblance to the leaf 'tentacles' of a *Drosera*. At the same time the setae gradually move from a vertical into a horizontal position ; and, during this process, the swellings at their bases (which, as will be seen later, are really pulvini) disappear. The tiny fruits are now fully exposed, and are ready to attach themselves to any passing animal (Fig. 3) [2].

Under a low power of the microscope, the pappus bristles have the appearance shown in Fig. 4, each being crowned by a number of capitate secretory hairs, set so closely together as to form a continuous gland. The capitate hairs (Fig. 5), which are of a type not uncommon in the Compositae [3], extend further down the seta on its exterior than they do on the side next to the corolla. Similar glandular hairs, but longer and narrower than those of the pappus, are found on many other parts of the plant, e. g., the lower part of the corolla, and the pericarp wall (Fig. 4), also on the peduncles, leaves, &c.

The secretion of the pappus-hairs is exceedingly sticky, and may retain (to a large extent) its adhesive power even after the fruits have been kept in a dry condition for some years. Water appears to have no effect on this secretion, though it readily dissolves in ether and some other solvents. It

[1] This species is widely spread throughout the tropics of both the Old and New Worlds, though the remaining four or five species of the genus are confined to the latter.

[2] Hoffmann figures (in Engler and Prantl's Pflanzenfamilien, Teil IV, Abt. 5, p. 132, Fig. 77, o) a fruiting capitulum of *A. viscosum* with the involucre not reflexed. This figure was probably taken from an immature capitulum, as in all cases, I believe, the involucre is finally reflexed.

[3] See Hanstein, Ueber die Organe des Harz- und Schleimabsonderung in den Laubknospen, Bot. Zeit., 1868, vol. xxvi, pp. 734 et seq., also Haberlandt, Physiologische Pflanzenanatomie, 2nd ed., Leipzig, 1896, p. 433.

stains a deep red with alcannin, and with osmic acid takes on a faint brown colour, though it is not blackened as an oil would be. In fact, it behaves generally like a body akin to resins, though, as seen above, it does not quickly harden, as an ordinary resin should. Possibly the secretion may be more or less allied to caoutchouc, or to the supposed caoutchouc-like substance which has received the name of 'Viscin [1].'

The pappus-setae are formed at a very early stage in the development of the flower. Each contains a single vascular bundle [2]; and, as the fruit matures, the walls of the cells surrounding this bundle become indurated and thickened, except in the region of the glandular hairs, and in the swollen base of the seta.

The structure of this basal swelling is interesting. It is composed, for the most part, of large, thin-walled cells (with no inter-cellular spaces), elongated in a direction at right-angles to the axis of the seta itself (Fig. 6). After the gland-stalks have assumed their final horizontal position, sections taken through the base of a seta show that these large cells have collapsed, their walls being much crumpled. This, together with the internal structure of the swelling, and the fact, observed in the field, that the swelling itself disappears during the movement of the gland-stalks, furnish, I think, sufficient proof that the dilated bases of the setae constitute the mechanism of movement. The base of each pappus-seta is in fact a pulvinus, composed largely of thin-walled motor cells, which probably act by losing water during the drying and ripening of the fruit.

The horizontal position assumed by the pappus-setae is probably advantageous in that it provides the fruit with a more extended (and therefore more secure) base of attachment.

In view of the fact that the feathery pappus of many Compositae executes similar movements, I examined some of our British species, with the result that, in a number of instances, a mechanism resembling that described above was found. In the cases examined, instead of the downward movement of the hairs being due, as stated by Haberlandt [3] (apparently for Compositae generally), to an unequal thickening of the walls at the bases of the hairs themselves, it was effected by means of a continuous annular pulvinus, on the edge of which the pappus hairs were borne (Figs. 7–9).

I have since found that two other authors (Talieff [4] and Hirsch [5]) have

[1] Cf. Parkin, Observations on Latex and its functions, Ann. of Bot., 1900, vol. xiv, p. 203.

[2] The Composite pappus rarely contains vascular tissue. Hoffmann, loc. cit., p. 97, states that only in some four genera (amongst which he does not mention *Adenostemma*) have even traces of vascular bundles been found in the pappus.

[3] Haberlandt, loc. cit., p. 465.

[4] Talieff, Ueber das hygroskopische Gewebe des Compositen-Pappus—abstract by Rothert: Bot. Centralblatt, 1895, vol. lxiii, p. 320.

[5] Hirsch, Ueber den Bewegungsmechanismus des Compositen-Pappus. Dissertation, Würzburg Berlin, 1901.

fully described this hygroscopic tissue in the Compositae, so that my results merely confirm their more extended observations. Hirsch[1] states that though in the majority of cases movement is effected by a pulvinus ('Polstergewebe'), yet in a few instances it is brought about by special motor cells in the basal parts of the hairs themselves.

Two kinds of hairs are found on the corolla; glandular capitate hairs, which occur only on the lower part, and long filamentous hairs, which are confined to the upper region, just below the corolla-lobes (Fig. 4). This second type of hair is not found elsewhere on the plant. In the bud, the florets are so close to each other, that the growth of these long filamentous hairs, during their development, results in those of one corolla being entangled with those of all the adjacent corollas. A dense felt of interwoven hairs is thus formed, which effectually ties together all the corollas of one capitulum (Figs. 1 and 2). The falling of the corollas *en masse*, which is the result of their being bound together in this manner, is probably of considerable importance; for if they fell separately, there would be a risk of some corollas being caught by the secretion of the pappus, and so impeding the action of the latter in respect to passing animals.

Hooker[2] noticed that the corollas fall off in a mass in some species of *Adenostemma*, but attributed this to their adhering together by their viscid surface. In this I think he was mistaken, as the lower parts of the corollas, which alone could be reached by the secretion of the hairs, are invariably free from each other (Fig. 2). Other species of *Adenostemma* have similar filamentous hairs on their corollas[3], which probably serve the same purpose.

In *Taraxacum officinale* and some other Composites, the corollas tend to fall, after withering, more or less in one mass. In these cases, however, the corollas merely adhere slightly to one another during drying, or at most are entangled by their ligulate tips.

Not only are the corollas bound together, but special arrangements exist, by means of which both they and the styles are cut off from the ripe fruits, and the latter are separated from the torus. In each case, during the ripening of the fruit, the walls of certain cells become thick and woody. This serves to give a special rigidity to these parts of the flower or fruit, while the adjacent parts, whose cell-walls remain thin and delicate, are easily ruptured. The direction of rupture is determined by the relative positions of the hard and soft tissues.

Thus in the corolla, a cylindrical mechanical layer is formed, by the thickening of the outer epidermis of the whole of its lower part. A few cells of the calyx-ring just below the corolla also become thickened. Abscission is then effected by the rupture of the thin-walled cells at the extreme base of the corolla (Fig. 10). Similarly the epidermis of the lower

[1] Hirsch, loc. cit., p. 38. [2] W. J. Hooker, Icones Plantarum, 1840, vol. iii, tab. 239.
[3] See figures in Martius and Eichler, Flora Brasiliensis, 1873–6, vol. vi, Part II, t. 51 and 52.

part of the style forms a cylinder of thickened cells. Separation in this case occurs by the breaking down of the thin-walled tissue at the base of the style (Fig. 10).

The fruits themselves are separated from the torus in a manner essentially similar to that described for the abscission of the corolla and style. Each fruit is attached to the base of a shallow pit in the torus, and is detached by the breaking down of fragile parenchymatous cells lying between the thick-walled epidermis of the lower part of the fruit, and a funnel-shaped layer of thickened cells of the torus (Fig. 11). Only those cells which form the rim of this 'funnel' are epidermal, the remaining cells being of a more deeply seated origin[1].

The vascular strand which supplies the ovary contains but few vessels, but is accompanied by numbers of short sclerotic cells (Fig. 11), which probably help to render the strand itself more brittle. In any case, the strand breaks across with great readiness.

In all these cases, the actual thickening of the cell-walls (including those of the sclerotic cells mentioned above) takes place only during the maturation of the fruit.

As we have seen, the process of fruit-dispersal in *Adenostemma* is facilitated by the abscission of certain parts of the flower, and later, of the fruit itself: and moreover, that this is aided by the topographical relations of hard and soft tissues. But such relations really do little more than determine the direction of rupture. The actual breaking down of the fragile tissues is probably due partly to their desiccation as the fruit ripens, and partly to the mechanical strains set up by such causes as the increasing convexity of the torus (Figs. 1–3).

The term 'absciss-layer,' which has sometimes been used in speaking of corollas[2], would appear to be, in cases such as that described above, somewhat of a misnomer. In those instances where (as in many Onagraceae) a definite meristematic layer is formed in connexion with the cutting off of parts of the flower, the term might be retained. But where separation of an organ depends more on the relative disposition of hard and soft tissues than on meristematic activity, some such term as 'absciss-mechanism' would seem preferable.

Although, as stated at the commencement of this paper, the genus *Adenostemma* appears to be unique in possessing a glandular pappus, yet certain other Compositae have glandular structures which aid, more or less effectively, the process of fruit-dispersal. Of these, the genus *Siegesbeckia*, which has glandular hairs on the involucral bracts, appears to be the most

[1] Not (at least in *Adenostemma*) merely epidermal, as stated by Kraus, Ueber den Bau trockner Pericarpien. Pringsheim's Jahrb. f. wiss. Bot., 1866, vol. v, pp. 123–4.

[2] Von Mohl, Ueber den Ablösungsprocess saftiger Pflanzenorgane, Bot. Zeitung, 1860, vol. xviii, p. 276, speaks of certain corollas as possessing an absciss-layer (Trennungsschicht), but he nowhere describes its structure.

interesting[1]. Cases, also in the Compositae, in which the fruit itself becomes mucilaginous, are described by Darwin[2] and Hildebrand[3]; while a number of instances are given by various authors[4], of plants of other natural orders whose fruits are said to be dispersed through the agency of animals, by means of glandular hairs situated on pericarp, calyx, bracts or other organs. But so far as I know, in none of these cases (except perhaps in *Siegesbeckia*) is the adaptation so complete as in the one which forms the subject of this paper.

In conclusion, I wish to thank Mr. Ridley, director of the Botanic Gardens, Singapore, and Mr. Macmillan, Curator of the Peradeniya Gardens, Ceylon, for kindly sending me a supply of both spirit material and ripe fruits of *Adenostemma*, that which I had myself collected having unfortunately been lost in transit.

[1] Hildebrand, loc. cit., pp. 12, 13, also Buchenau, Ueber Blüthenentwickelung bei den Compositen, 1872, Bot. Zeit., vol. xxx, p. 366, with Taf. V, figs. 19–27.

[2] C. Darwin, Note on the Achenia of *Pumilio argyrolepis*, Gard. Chron., 1861, p. 4.

[3] Hildebrand, Ueber die Verbreitungsmittel der Pflanzenfrüchte durch Haftorgane, Bot. Zeit., 1872, vol. xxx, p. 910.

[4] See Kerner and Oliver, Natural History of Plants, London, 1894, vol. ii, pp. 869, 870; also Hildebrand, loc. cit. (two papers), and Die Verbreitungsmittel der Pflanzen, Leipzig, 1873, pp. 88 et seq.

EXPLANATION OF PLATE XXIII.

Illustrating Prof. Yapp's paper on Fruit-dispersal in *Adenostemma viscosum*.

All the figures except 7–9 refer to *Adenostemma viscosum*, Forst.

Fig. 1. A flowering capitulum cut vertically through the middle. × 3.

Fig. 2. A later stage. The involucral bracts are becoming reflexed, and the corollas, bound together by the hairs at their apices, are in the act of falling off in one mass. × 3.

Fig. 3. Fruiting stage. The involucre is completely reflexed, and the fruits (only 5 of which remain) fully exposed. The tip of each pappus-seta is surrounded by a drop of viscid secretion. × 3.

Fig. 4. Part of a single floret, showing the calyx-ring and two stalked glands, each with a pulvinus (*p*) at its base. Note the filamentous hairs on upper part of corolla, and the glandular hairs on the pericarp, pappus-setae and lower part of corolla. × 30.

Fig. 5. Three mature glandular hairs from a pappus-seta, as seen in a longitudinal section of the latter. Note the density of the cell-contents of both hairs and epidermis. × 360.

Fig. 6. Longitudinal section through the dilated base (pulvinus) of a pappus-seta, *m. c.* motor cells, *cor.* corolla. × 140.

Fig. 7. Fruit of *Hypochoeris radicata*, before expansion of pappus, *p.* annular pulvinus. × 2.

Fig. 8. Do. after expansion of pappus. Note the flattened pulvinus, *p.* × 2.

Fig. 9. *Tragopogon pratense*. Longitudinal section through the apex of the beak of a fruit, showing the annular pulvinus, *p.* *K.* pappus. × 90.

Fig. 10. Longitudinal section showing the abscise-mechanisms of the corolla and style in *Adenostemma*. N.B. The thick-walled cells are shaded. *cor.* corolla, *n*, nectary, *st.* style. Corolla ruptures at *a*, style at *b. b.* × 140.

Fig. 11. Longitudinal section to show abscise-mechanism of fruit; *ep.* thick-walled epidermis of base of fruit; *f.* funnel-shaped layer of mechanical cells connecting epidermis of torus with the vascular strand; *t*, thin-walled tissue which initiates the rupturing process. × 100.

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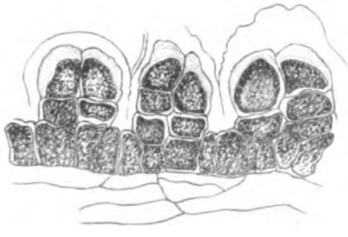

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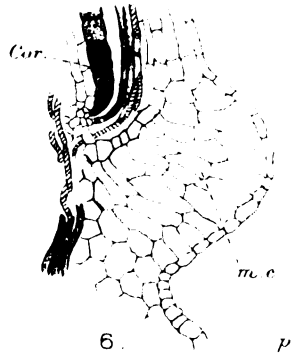

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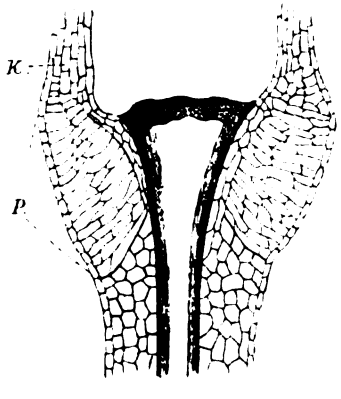

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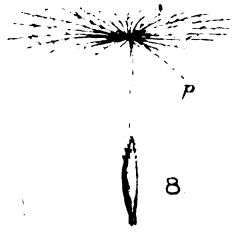

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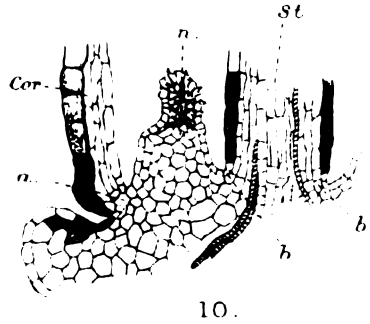

10.

YAPP — ADENOSTEMMA VISCOSUM.

NOTES.

THE STRUCTURE OF LEPIDODENDRON OBOVATUM, STERNB.—It rarely happens that the palaeobotanist has the opportunity of investigating the anatomical structure of a specimen which at the same time exhibits external characters allowing of its specific determination. In the present preliminary note I propose to place on record a case of this kind which has recently come under my observation.

On December 15, 1904, I received from Mr. J. Parker, of Earby, near Colne, Lancashire, among other specimens from the Lower Coal-measures at Towneley, the petrified stem of a *Lepidodendron*, from which the matrix had split away in such a manner as to expose a part of the external surface of the plant. The exposed surface is completely clothed by the leaf-bases, of which about twenty are visible; they are not flattened, as is usually the case in the ordinary casts, but stand out in strong relief. The scar from which the leaf had fallen is plainly seen at the top of each cushion, and the cushion itself has a well-marked median rib. On either side of the rib the lateral prints can in some cases be clearly seen; the markings on the scar itself are somewhat obscure. The detached portion of the matrix, giving the mould of the surface, shows the corresponding features clearly. The general outline of the leaf-cushions is rhomboidal with rounded angles; the slope of the lateral surfaces towards the rib, together with that of the scar above, gives the whole somewhat the form of a three-sided pyramid, modified, however, by the fact that the rib itself has a concave curvature.

The plant was evidently capable of specific determination, and with this view I submitted the specimen to the highest systematic authority in this country, Mr. R. Kidston, F.R.S., who kindly examined it, and states in a letter dated March 17, 1905, 'The specimen showing structure is without doubt *Lepidodendron obovatum*.'

The species having thus been satisfactorily identified, I sent the block to Dr. Krantz, of Bonn, to have sections cut, taking care that the part showing the superficial characters should be preserved uninjured.

In addition to the branch (A) of which the surface was exposed, the block contained another specimen, evidently of the same nature, but immersed in the matrix. Sections were prepared from both branches, which proved to be united below, forming part of the same dichotomizing stem.

The branch A showing the surface measures about 50 × 30 mm., the other is somewhat larger, having a diameter of about 65 × 25 mm. in its present condition, the leaf-bases being included in each case. The preservation is very fairly good. The stele has a medulla, enclosed within the broad ring of primary centripetal wood, which does not show any specially well-marked corona. Surrounding the primary

wood is a zone of radially arranged tissue, evidently of secondary origin, and occupying the place of the secondary xylem. I have not, however, been able to detect any tracheides in this zone, which appears to be wholly parenchymatous, except of course where the leaf-traces pass through it. The presence of this parenchymatous zone is characteristic of the type of stem commonly referred to *Lepidophloios fuliginosus*; in some specimens of the latter type groups of secondary tracheides are embedded in the secondary parenchyma, while in other cases the structure has been found to be entirely parenchymatous, as in the fine Halonial branch which Professor Weiss refers to *Lepidophloios fuliginosus*.[1] I have found the specimens in my collection extremely variable in this respect, the tracheides, where they appear, being sometimes quite local in their occurrence.

The phloem-zone in our specimen of *Lepidodendron obovatum* is imperfectly preserved; beyond this we come to the inner cortex, a comparatively narrow zone of dense, small-celled tissue; outside this the broader middle cortex is partially preserved, and consists of a delicate tissue of relatively large cells. The outer cortex has a firmer structure, resembling the inner cortex in this respect, but with rather larger cells. The leaf-bases present the usual structural features—vascular bundle, parichnos, and ligular pit. Within the leaf-bases the zone of periderm, usual in *Lepidodendreae*, is well developed; in branch A a second peridem, internal to the first, is present locally.

The leaf-traces are met with in all parts of their course from the stele to the leaf-bases; they are often well-preserved, and show exactly the same structure as has been figured in stems referred to *Lepidophloios fuliginosus*.[2] The presence, on the phloem-side of the strand, of the dark mass or crescent, interpreted by Mr. Seward as secretory tissue, is a striking point of agreement.

In branch A there is a specially interesting feature in the presence of a small lateral stele, which, in the three transverse sections of this specimen, is shown at three points of its outward course. The small stele has a somewhat horse-shoe form at first, gradually closing up into a circle as it passes further outwards. The wood appears to enclose a small pith, and leaf-traces are given off while the stele is still on its way through the parent cortex. There is a very marked resemblance to the steles supplying Halonial tubercles, as shown, for example, in Professor Weiss's specimen. The main stele remains open on the side from which the lateral stele has been given off, the gap becoming narrower upwards, but not closing within the region from which sections have been cut.

The most striking point about the structure of the stem of *Lepidodendron obovatum* is its close agreement with that of *Lepidophloios fuliginosus*. If the specimen had been found in the usual condition, without superficial characters, it would beyond doubt have been placed in the genus *Lepidophloios*, if not in the species *L. fuliginosus*. The fact that our stem is clearly referable to a typical species of *Lepidodendron* shows that external and anatomical characters do not necessarily correspond in the Lepidodendreae, and warns us that all identifications of *Lepidophloios*

[1] F. E. Weiss, A Biseriate Halonial Branch of *Lepidophloios fuliginosus*, Trans. Linn. Soc. London (Bot.), vol. vi, 1902, p. 225.

[2] Seward, Notes on the Binney Collection of Coal-Measure Plants, Part I, *Lepidophloios*. Proc. Cambridge Phil. Soc., vol. x, 1899, Pl. III, Figs. 1 and 2. Weiss, l. c., Pl. XXV, Fig. 13.

based on anatomical features are open to suspicion. From the examination of specimens in my own collection, I have no doubt that quite heterogeneous stems are commonly confounded under the name *Lepidophloios fuliginosus*. Some, no doubt, like that originally identified by Messrs. Cash and Lomax[1], really belong to *Lepidophloios*, but others are in all probability referable, like the specimen now described, to species of *Lepidodendron*. Internal structure is presumably of more importance than external configuration, and we may conjecture that the characters of the leaf-bases, on which systematists have been compelled to rely, possess but small taxonomic value.

D. H. SCOTT.

KEW.

LIGNIFICATION OF PHLOEM IN HELIANTHUS.—Some observations on the phloem of the common sunflower were described in a note[2] published in 1902; the chief points were as follows. In an old stem, collected early in October of the previous year, it was found that lignification of the walls had taken place in a considerable number of sieve-tubes and companion-cells, as well as in many of the phloem-rays, and in the whole of the pericycle; the rather surprising result was also obtained, that the proteid-contents of some sieve-tubes and companion-cells gave lignin-reactions[3], especially in the root, where lignification of the walls of these elements was not observed.

These results were based on an examination of two plants only, and required to be supplemented by further observations. For this purpose additional material was collected in 1902 for future investigation, and included eleven plants of *Helianthus annuus*, L., one plant of *H. tuberosus*, L., and stems of *H. laetiflorus*, Pers., and *H. decapetalus*, L. All of these except the specimen of *H. tuberosus* were grown at Kew. The object of the present note is to give the results of the examination of this material.

The lignification previously observed appears to be of general occurrence in old stems of the sunflower, since the walls of a large number of sieve-tubes and other elements of the phloem proved to be lignified in all the specimens of this species; the same was observed in the three other species of *Helianthus* mentioned above. The contents of numerous sieve-tubes and companion-cells were lignified in the root of all the sunflower-plants and in that of *H. tuberosus*[4]. Thus the previous observations are confirmed for the sunflower, and extended to other species of the same genus.

Of the eleven plants of the sunflower, nine were grown close together and at first treated alike, but two of them were transferred to a green-house in August, and from two other plants the different capitula were successively removed before reaching

[1] W. Cash and J. Lomax, On *Lepidophloios* and *Lepidodendron*, Report of the British Association (Leeds), 1890, p. 810.

[2] Boodle, On lignification in the phloem of *Helianthus annuus*, Annals of Botany, vol. xvi, p. 180.

[3] The different reagents used are mentioned on p. 181, loc. cit.

[4] The roots of *H. laetiflorus* and *H. decapetalus* were not examined.

any considerable size. These two plants were left growing until December 12, their upper leaves, which had remained green, having been killed by a frost a few days previously. The other plants were collected at different times from October 15 to December 6, in each case after the fruiting of the main flower-heads had been completed.

The proportional amount of lignified tissue was found to vary greatly in different plants, and in different parts of the same plant. In most cases lignification of the phloem is more general in the upper part of the stem than near the base (e.g. two inches above the level of the soil), the middle region being intermediate. The pericycle behaves similarly, the whole or the greater part of this tissue being lignified in the upper region of the stem, while at the base usually very little of it had undergone lignification, or sometimes none.

In the plant showing the greatest amount of lignification, there were, at intervals, small groups of elements having cellulose walls and consisting of two or three sieve-tubes with companion-cells, while opposite the primary masses of sclerenchyma similar but rather larger groups were present; apart from these the whole of the phloem and pericycle had become lignified. No cambium remained, so that a transverse section showed a continuous mass of lignified tissue, comprising the xylem and the tissues between the latter and the endodermis [1], and interrupted only by small islands of unaltered phloem.

Lignification of the phloem generally begins immediately on the inner side of the primary groups of sclerenchyma, and proceeds from these towards the xylem. Usually the medullary rays in the phloem undergo gradual lignification from within (i.e. from the limit of the xylem) outwards, and this often begins a little later than in the first phloem-elements. The groups of sclerenchyma may become connected with the xylem by bridges of lignified tissue at a time when there is very little lignified tissue at intermediate points. As a rule lignification of the pericycle begins, often comparatively late, at the sides of the groups of sclerenchyma, and proceeds tangentially. Hence it appears that in all these tissues lignification generally takes place in elements adjacent to previously lignified tissue.

From the data obtained it was not found possible to deduce the cause of lignification of the phloem. The largest plant (stem eight feet high, and 3·8 cm. in diameter at the base) showed the greatest amount of lignification in the basal region, and the smallest plant (stem three feet high, and less than 1 cm. in diameter at the base) showed the least amount, but the remaining plants gave no sort of proportion between the degree of lignification and the size of the stem. Neither was there a regular relation to the age of the plants. Again the two plants, from which the flower-buds were cut off, showed less lignification at the base of the stem than the majority of the other plants, but the distinction was not sufficient to warrant any definite conclusion. Possibly lignification of the walls may set in near the time of the death of the elements, and this may depend on several factors affecting the supply and demand of food-substances.

Lignification of the proteid contents of sieve-tubes was seen in the roots of all

[1] Lignification appears to stop accurately at the endodermis; no cases of lignified cortical cells were observed.

the specimens [1]. It was sometimes only to be observed for a short distance from the sieve-plate, but in other cases extended throughout the length of the element. It was found to occur in sieve-tubes where the callus formed a very thick deposit on the sieve-plates, as well as in others where no callus was present. The walls of some few sieve-tubes in the root were slightly lignified (chiefly close to the sieve-plate) in two or three plants, but no general lignification of the phloem in the root was observed.

From the observations described above it appears that the walls of the phloem-elements in the stem, and the contents of the sieve-tubes in the root become normally lignified in the sunflower, and the same phenomena occur in other species of *Helianthus*. The occurrence of lignified contents in the sieve-tubes of the root of *H. tuberosus* shows that this feature is not restricted to annual species.

L. A. BOODLE.

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GERMINATION OF THE SPORES OF OPHIOGLOSSUM.—During a recent visit to Java, attempts were made by the writer to germinate the spores of several species of Ophioglossum. Three species—*O. Moluccanum*, *O. intermedium*, and *O. pendulum*, germinated, and in all of these the earliest stages were observed.

O. Moluccanum germinates very freely and quickly, the first germination stages having been met with within three days. In this species a small amount of chlorophyll was sometimes found, but it was insufficient to enable the young prothallium to develop independently, and the largest ones had but four cells.

Germination in *O. intermedium* was much slower. Only a small amount of this rare species was available, and the observations were necessarily very incomplete. About a month after the spores were sown, the first stages were found. No chlorophyll could be detected, and the prothallia had but three cells.

Spores of *O. pendulum* collected at Hanwella in Ceylon, and at Tjibodas in Java, were sown, and germinations were obtained in both cases. The first stages were not met with until about a month after the spores were sown, but it is quite possible that some may have germinated sooner.

As in *O. intermedium*, no chlorophyll was formed, and the development of the young prothallium, until three cells were formed, was very much the same. But in *O. pendulum* a number of young prothallia were found, in which there was an association with a mycorhizal fungus, which penetrated the cells of the young prothallium, and caused its further development. In one case a young prothallium of thirteen cells was found. In every case where growth had advanced beyond a three-celled stage, the mycorhiza was present.

A number of adult prothallia of *O. Moluccanum* were found at Buitenzorg; and at Tjibodas prothallia of *O. pendulum* were collected in the humus between the leaf-bases of *Asplenium nidus*.

DOUGLAS H. CAMPBELL.

SINGAPORE,
June, 1906.

[1] Mr. J. H. Van Stone informed me in 1902 that he had observed lignification of the contents of some of the sieve-tubes in the stem of the perennial sunflower.

MULTIPLE CHROMATOPHORES IN ANTHOCEROS.—In 1897 the writer collected in Jamaica a sterile fragment of an *Anthoceros*, in which the superficial cells showed two chromatophores instead of the single one characteristic of the Anthocerotes. Since that time, repeated search has been made for similar species, but hitherto without success.

In Ceylon various species of *Anthoceros* were collected, but none showed any deviation from the ordinary type.

While in Buitenzorg, an *Anthoceros* was found in the Tjiapus Gorge at the base of Mount Salak, which showed frequent instances of double chromatophores in the superficial cells. An examination of the inner tissue of the thallus revealed the presence of multiple chromatophores in all the cells. There were not infrequently as many as eight in a cell.

The same species (or a closely related one) was afterwards collected at a number of places near Tjibodas where it was not at all uncommon.

This species belongs to the section of the genus with spiral elaters and no stomata in the sporophyte. In both respects it comes nearer *Dendroceros* than *Anthoceros*, although the thallus is that of a typical *Anthoceros*.

All of the Javanese specimens showed also a solitary antheridium, and chlorophyll in the ripe spores, also suggestive of *Dendroceros*.

The pyrenoid, usually so conspicuous in the chromatophores of the Anthocerotes, seems to be quite absent, and in this respect, as well as in the increased number of the chromatophores, there is a close approach to the chromatophores of the other Archegoniates.

The plants usually grew on rotten logs, but were also met with on earth and damp rocks.

If it should prove that all of the species belonging to the section of *Anthoceros* with spiral elaters and no stomata have multiple chromatophores, it will probably be found necessary to separate them as a new genus, intermediate to some extent between *Anthoceros* and *Dendroceros*.

DOUGLAS H. CAMPBELL.

SINGAPORE,
June, 1906.

A Review of the genera Meconopsis and Cathcartia.

BY

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With Plates XXIV and XXV.

1. MECONOPSIS.

HISTORY.

THE name *Meconopsis* was proposed by Viguier in 1814 (Hist. Pav. Diss., 20) for the plant known familiarly in this country as the Welsh Poppy. By the earlier systematists this plant was sometimes treated as a *Papaver*, sometimes as an *Argemone*. When included in *Argemone* it will be understood that the genus intended was not the *Argemone* of modern botanical works, first clearly defined by Tournefort in 1694, but the pre-Tournefortian *Argemone*, all the species of which Tournefort relegated to *Papaver*[1]. The limitation of *Papaver* and *Argemone* which Tournefort advocated was substantially adopted by Linnaeus, who, in 1753 (Species Plantarum, ed. 1), named the Welsh Poppy *Papaver cambricum*.

Viguier's proposal, and his name *Meconopsis cambrica*, were adopted in 1815 by De Candolle (Flor. Fr., ed. 3, v. 586), but in spite of this sponsorship a generation elapsed before either the name or the view found acceptance. In 1816 Desportes (Dict. Sci. Nat., ii. 481), while assenting to the removal of the Welsh Poppy from *Papaver*, did not admit the necessity for a genus *Meconopsis*, but referred the plant to *Argemone*, as *A. cambrica*. In this case, however, it was in the new or Tournefortian *Argemone*, not in *Argemone* as understood by the early writers, that Desportes placed the Welsh Poppy. The arrangement is not a happy one, for it obscures Tournefort's *Argemone* without making Viguier's *Meconopsis* intelligible. When in 1821 De Candolle dealt again with the plant (Syst. Veg., ii. 87) he gave no support to Desportes' view. However, while disposing of one difficulty De Candolle created another, because he linked with Viguier's

[1] For a detailed history of the change of incidence of the name *Argemone*, see Journal of Botany, xxxiii, pp. 130–2.

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genus two forms of an American Celandine on which in 1818 Nuttall had based his genus *Stylophorum* [1]. This treatment, which obscures the limits of *Meconopsis* as Desportes' had obscured those of *Argemone*, was repeated by De Candolle in 1824 (Prodr., i. 121). In the following year D. Don (Prodr. Fl. Nepal., 196) returned to the view of Tournefort and of Linnaeus and treated certain species of *Meconopsis* as *Papavers*. However, in 1827, Sprengel (Syst., ii. 570) accepted De Candolle's view as to the relationship of *Meconopsis*, Vig., and *Stylophorum*, Nutt., but in doing so added a bibliographical difficulty to the taxonomic one, because he decided to reduce Viguier's earlier name and to employ Nuttall's later one for the composite genus. This *bouleversement* was accepted by G. Don in 1831 (Gen. Syst., i.), and although Bernhardi in 1833 (Linnaea, viii. 462) restored *Meconopsis* to its proper position, the confusion was perpetuated by Steudel (Nomencl., ed. 2, ii.) in 1841, nor was it till A. Gray showed in 1848 (Gen., i. 114) that Nuttall's *Stylophorum* is not congeneric with Viguier's *Meconopsis* that the latter name came into general use.

The first genuine *Meconopsis* to be added to Viguier's genus was *M. napaulensis*, described by De Candolle (Prodr., i. 121) in 1824; it has, however, to be noted that De Candolle treated it as a doubtful species, and that he placed it in his section *Stylophorum*, which should never have been included in the genus, not in *Meconopsis* proper. In 1825 D. Don described two others, also from Nepal (Prodr. Fl. Nepal., 196). One of them Don supposed to be identical with *M. napaulensis*; both he treated as species of *Papaver*. All three Nepalese species had been collected by Wallich, who issued them, with two others, from the Himalayan region but not from Nepal, in 1830 (Lith. Cat., nn. 8121–25) as unnamed species of *Meconopsis*. The identity of the Wallichian *Meconopses* will be given in dealing with the group *Robustae*.

A few years later Bentham, in 1835, described two additional forms from California. These two, *M. heterophylla* and *M. crassifolia*, have given a good deal of trouble to Californian botanists. It appears to be generally admitted that there are really two distinguishable stylate 'Poppies' in California, but it seems to be doubtful whether they represent two forms of one species differing in facies in consequence of their environment (Flor. Francisc., 281), two distinct varieties of the same species (Flor. West Mid. Calif., 209), or two different species (Bot. San Francisc. Bay, 9).

A fourth Himalayan species, which is included in the list of those issued without specific names by Wallich, was described as *M. aculeata* by Royle (Ill. Him. Pl., 67) in 1839. It was not till 1852 that another Himalayan species, the fifth from the Himalaya and the eighth species in the genus, was described by Sir W. Hooker (Bot. Mag., t. 4668). This last

[1] This complication, from the point of view of *Stylophorum*, is disentangled in Bulletin de l'herbier Boissier, iii, p. 573.

species came from the Sikkim Himalaya, and although Sir W. Hooker identified with it one of Wallich's Nepalese *Meconopses*, it happens that this particular species, which Hooker termed *M. Wallichii*, has not yet been reported from Nepal and never was collected or seen by Wallich. The next addition to the genus was made in 1855 (Fl. Ind., 251–4) by Hooker and Thomson, who then dealt with and accounted for all but one of the unnamed *Meconopses* issued by Wallich in 1830, and described two new species, making seven for the Himalaya and ten for the whole genus. Of these new species, one (*M. robusta*) was already, though without a name, in Wallich's collection, the other (*M. horridula*) was not. No further additions were made to the genus till 1876, when Regel (Gartenfl., xxv. 291) described *M. quintuplinervia*, the first species to be reported from China. In the same year Maximowicz described two others from China and North-East Tibet (Mel. Biol., ix.), though one of these appears to be no more than a form of the Himalayan *M. horridula*; the other (*M. integrifolia*) Maximowicz treated in the first instance as a *Cathcartia*. To these Chinese species Franchet in 1886 added two (*M. Delavayi* and *M. lancifolia*), which he treated as species of *Cathcartia*; Maximowicz in 1889 added a fifth (*M. punicea*), and Franchet in 1891 added two more (*M. Henrici* and *M. chelidonifolia*). In 1894 the writer described the Himalayan *M. bella*, thus bringing the total for the Himalaya to eight, and for the whole genus to eighteen. In the following year the writer dealt with four additional Himalayan species (*M. primulina*, *M. sinuata*, *M. superba*, and *M. grandis*) and with another Chinese species (*M. Oliveriana*), bringing the Himalayan species up to twelve, the Chinese to eight, and the total for the genus to twenty-three. Another Himalayan species and three more Tibetan or Chinese species have now to be reported, raising the total number of distinguishable forms to twenty-seven.

MORPHOLOGY.

The Himalayan species of the genus have already received some attention on the writer's part [1], and in dealing with these incidental reference has been made to some of the Chinese ones. The necessity that has arisen for the preparation of descriptions of the four additional species just mentioned calls for further discussion of the genus as a whole, and the present opportunity is taken of enumerating and reviewing all the species.

A typical *Meconopsis* such as the Welsh Poppy, *M. cambrica*, Vig., on which the genus was founded, or the blue Sikkim Poppy, *M. Wallichii*, Hook. (Pl. XXIV, Fig. 6), is easily distinguished from a true *Papaver*, like *P. somniferum*, Linn., or *P. dubium*, Linn. (Pl. XXIV, Figs. 1, 2). In both genera, as is shown in Pl. XXIV, drawn by Miss M. Smith, the ripe

[1] Journ. As. Soc. Beng., lxiii. 2, 81–2 (1894), and lxiv. 2, 309–21 (1895); Ann. Roy. Bot. Gard. Calcutta, ix. 1, 2–5, tt. 2–6 (1901); Gard. Chron., ser. III, xxxvii. 369–70 (1905).

capsule dehisces under the apex by means of short more or less transverse valvular chinks between the placental ribs. In the species of *Papaver* referred to, the vertex of the capsule is a definite disk bearing on its upper surface the radiating stigmas and more or less concealing by its projecting margin the chinks through which the seeds escape. In the species of *Meconopsis* cited the capsule has no disk, the chinks by which it dehisces are unconcealed, and the apex ends in a persistent style, crowned by the clavate or subcapitate slightly lobed stigma.

The two genera are, however, closely allied, and from the time of Tournefort (1694) till that of Viguier (1814) they were united. The differences between the two are not always so clearly defined as in the examples quoted; there are species of *Papaver*, like *P. polychaetum*, Schott and Kotschy (Pl. XXIV, Figs. 3, 4), one of the species of *Papaver* which constitute the section *Miltantha*, and correspond more or less to the pre-Tournefortian genus *Argemone*, where the chinks of dehiscence are not hidden by a projecting disk-margin; there are other species, like *P. stylatum*, Boiss. and Bal. (Pl. XXIV, Fig. 5), in the Old World, and like *P. Lemmoni*, Greene, in the New, where the disk projects into a distinct central style. On the other hand, a whole group of species of *Meconopsis*, the *Grandes*, has the stigma as definitely radiating as in any *Papaver*; in two species of this group, *M. punicea*, Maxim., and *M. integrifolia*, Franch. (Pl. XXIV, Figs. 7, 8), the stigma is not even separated from the body of the capsule by an intervening style; here, however, there certainly is no disk.

Again, in the Californian group of *Meconopsis*, the *Anomalae*, we find that at the base of the distinct style the vertex of the capsule is flattened and disk-like (Pl. XXIV, Figs. 9, 10). Here, however, there is not a disk such as we have in *Papaver dubium* with a margin projecting beyond the transverse chinks through which the seeds are discharged; we have merely a flattening of that portion of the capsule, in this case somewhat extensive, which is interposed between the apices of the valves and the base of the style. The same feature, though not to so exaggerated an extent, and with the portion between apices of valves and style-base convex instead of flat, is met with in *M. bella*, Prain. In one *Meconopsis*, however, *M. primulina*, Prain, we find that on alternate, but not on all the placental ribs there are, at the base of the style, epaulette-like outgrowths which suggest the rudiments of a projecting disk-margin. It has now to be recorded that in two species of *Meconopsis*, *M. torquata*, Prain (Pl. XXIV, Fig. 11), and *M. discigera*, Prain (Pl. XXIV, Fig. 12), described for the first time in the systematic portion of this paper, the capsule is surmounted by a true disk, the margin of which projects, as in a typical *Papaver*, beyond the series of chinks by which the seeds find egress.

We have seen that in 1825 D. Don (Prodr. Fl. Nepal., 196) did not consider the absence of a disk and the presence of a style sufficient justifica-

tion for the recognition of *Meconopsis* as generically distinct from *Papaver*. In 1888 Greene (Pittonia, i. 168) had occasion to discuss the nature of the gynoecium in three Californian species: *Papaver californicum*, Gray, which has a disk like that of *P. dubium*; *P. Lemmoni*, Greene, where the vertex of the capsule, from his description, is like that of *P. stylatum*; and the plant taken by Greene to be *Meconopsis heterophylla*. Owing to the somewhat intermediate nature of the gynoecium of *Papaver Lemmoni*, Greene has decided, as Don had decided more than sixty years before, that the recognition of the genus *Meconopsis*, as distinct from *Papaver*, is uncalled for. In this view he has been followed by Jepson (Flor. West Mid. Calif., 209). From what has been said above, and from an examination of the figures in Pl. XXIV, it will be seen that the position of Don and Greene and Jepson is perhaps stronger than any of them had reason to believe.

In spite, however, of the weight of authority on the other side, the writer feels that it would be inconvenient, even if it were necessary, to adopt the suggestion made by Don and revived by Greene. Had it been merely a matter of dealing with the original European *Meconopsis* and the Californian forms, the conclusion might have been accepted and the species in question treated as aberrant *Papavers*. But we have to deal with four-and-twenty Asiatic forms as well, and in considering these we have to face another troublesome question. The genus *Cathcartia*, as we now know, differs from *Meconopsis* by only one valid character: in *Meconopsis* the capsules open by apical chinks, in *Cathcartia* the valves split to the base. If *Meconopsis* is an unsatisfactory genus, *Cathcartia* too must go. So alike are the two, that authorities so great as Maximowicz and Franchet have taken *Meconopses* to be *Cathcartiae*, and the writer believes that one species described by Franchet as a *Meconopsis* is really a *Cathcartia*. But if *Cathcartia* disappears nothing can save *Stylophorum*, and *Stylophorum* is, after all, only *Chelidonium*. Nor can we stop here. There are species of *Papaver*, like *P. orientale*, Linn., with 3-merous flowers; species like *P. pavoninum*, Schrenk, with horned sepals; species like *P. horridum*, DC., and like *Meconopsis horridula*, Hook. f. and Thoms., with spinescent leaves and capsules. We therefore find, in the conjoined genera *Papaver* and *Meconopsis*, practically every character that marks Tournefort's genus *Argemone*. If we follow Don and Greene in the suggestion that Viguier's work be cancelled, we may find ourselves left without a landmark in the natural family Papaveraceae.

The occurrence of intermediate forms is not in itself a sufficient reason in all cases for the combination of nearly allied genera. To cite familiar instances where there really are intermediates, no one seriously thinks of uniting *Aconitum* and *Delphinium*, and few have been so bold as to advocate the reduction of *Cirrhopetalum* to *Bulbophyllum*. However, in the case now under consideration, the fusion which has been suggested is not

urgently called for on morphological grounds. In spite of the many directions in which the one genus approaches the other, the differences between them never absolutely disappear, and it is still not only possible but easy to distinguish any species of *Meconopsis* hitherto reported from every species of *Papaver* as yet described. All that seems necessary is some modification in the popular conception of both genera, and some amendment in the usual definition of *Meconopsis*.

It is not as regards the gynoecium alone that modification of idea and definition is required. In *Papaver*, while one or two species have 3 sepals and 6 petals, the majority have 2 sepals and 4 petals in two pairs, an arrangement so characteristic of the natural family Papaveraceae as to have received the name 'papaveroid.' With few exceptions[1] the definitions of *Meconopsis* credit the genus with this arrangement and number of parts. But although it be true that every *Meconopsis* so far known has only 2 sepals, one-third of the species have more than 4 petals; when this is so, the petals are disposed as they are in the genus *Sanguinaria*. This arrangement is met with in *M. horridula* (group *Aculeatae*); in *M. primulina*, *M. Henrici*, and *M. Delavayi* (group *Primulinae*); in *M. integrifolia*, *M. simplicifolia*, *M. grandis*, and sometimes in *M. punicea* (group *Grandes*). Even in those groups in which the arrangement occurs, it is not in any case characteristic of the whole group; it does, however, appear usually to be almost, if not quite, characteristic of individual species. In the systematic portion of this paper two more species, in which the corolla is 'sanguinarioid' and not 'papaveroid,' have to be dealt with.

During 1899–1901 a journey was made in Tibet by Capt. P. K. Koslov. Circumstances led to his wintering just below the level of the Tibetan plateau in the valley of the Ra-chu, one of the head-waters of the Mekong[2]. In this locality, situated approximately in lon. 97° 30′ E. and lat. 29° 30′ N., some of the members of Koslov's party made a collection of seeds for the Imperial Botanic Garden, St. Petersburg. A number of the seeds thus obtained were sent by Dr. Fischer de Waldheim to Mr. A. K. Bulley, Neston. Among the plants raised by Mr. Bulley was a *Meconopsis* (group *Grandes*) with sanguinarioid yellow flowers. This plant was figured by Mr. Bulley (Flora and Sylva, iii. 80) in 1905 as *M. integrifolia*, a species which it indeed resembles and to which it is nearly related, but from which it differs much as *M. simplicifolia* differs from *M. grandis*. Another example of this species, presented by Mr. Bulley to Kew, flowered in the Alpine Garden there in May, 1906. Having thus had an opportunity of studying it and *M. integrifolia* side by side in the living state, the writer has been able to confirm the opinion already expressed by Bulley (Flora

[1] Hooker and Thomson in their Flora Indica, published in 1855, were the first to give a correct definition.

[2] Journ. Roy. Geogr. Soc., xix. 589 (1902).

and Sylva, iii. 191) and by Hemsley (Bot. Mag., t. 8027) that this species is distinct from *M. integrifolia*. In the correspondence which has taken place regarding this plant, Dr. Fischer de Waldheim has invited the writer to name and describe the species. It is dealt with below as *M. pseudo-integrifolia* (Pl. XXV).

In 1905 Messrs. James Veitch and Sons kindly allowed the writer to examine the fine collection of *Meconopsis* made for them in south-western China by Mr. E. H. Wilson. This collection contained ample material of *M. chelidonifolia*, Bur. and Franch., and of *M. Oliveriana*, Franch. and Prain, two species that as regards their fruits are very distinct, but that in all other respects are puzzlingly alike. It is now certain that the flowers of *M. Oliveriana* are yellow, as they are in *M. chelidonifolia*, not purplish, as the writer in 1895 was inclined to believe. Another interesting fact brought out by this collection is that *M. Wallichii*, the blue Sikkim Poppy, extends to, or at all events reappears in, Szechuen. The collection also contains fuller material of *M. Henrici*, Bur. and Franch., a species described in 1891, which has this year (1906) flowered with Messrs. Veitch at Coombe Wood. A question has arisen with regard to this species which cannot for the moment be definitely settled, but which illustrates the difficulties that are encountered in dealing with species of this genus. In 1876 Maximowicz described for the first time the form known in gardens as *M. racemosa*. The writer has already (Journ. As. Soc. Beng., lxiv. 2, 314) shown that we have reason to believe that *M. racemosa* is only a form of *M. horridula* with agglutinated instead of discrete scapes. An opportunity since 1895 of examining both forms as they grow, side by side, in southern Tibet has tended to confirm the writer in this opinion. Though it probably will be convenient in horticulture to continue the use of the name *M. racemosa*, there is hardly room for doubt that *M. racemosa* and *M. horridula* are conspecific. In 1886 Franchet described as a *Cathcartia* the *Meconopsis lancifolia* (group *Primulinae*) of this paper, a species which, like *M. racemosa* among the *Aculeatae*, has flowers in raceme-like cymes *without bracts subtending the individual flowers*. Now that fruiting specimens of *M. Henrici* are available it is found that its capsules are quite like those of *M. lancifolia*, and there is room for suspicion that *M. lancifolia* from Yunnan may bear to *M. Henrici* from Szechuen somewhat of the relationship that *M. racemosa* bears to *M. horridula*.

The receipt of further material of the plant, which in 1895 the writer dealt with as *M. sinuata*, var. *Prattii*, shows that it is not referable to *M. sinuata*. In *M. sinuata* there are 4 petals and the capsule is very like that of *M. Henrici*, whereas the form in question has 5–8 petals, and has a fruit more like that of *M. aculeata* and *M. horridula*, but smaller than in either of these species. It now appears that *M. sinuata*, var. *Prattii*, from Szechuen is identical with a plant from Yunnan which the writer treated as

a variety (var. *rudis*) of *M. horridula*. This plant, as was pointed out eleven years ago, is the *M. racemosa* of Franchet (Pl. Delavay., 41) but not the *M. racemosa* of Maximowicz. Now that more complete material is available it seems advisable to treat this Yunnan and Szechuen plant as a distinct species of the group *Aculeatae*. The writer has already pointed out that *M. horridula*, with its variety *racemosa*, is virtually a Tibetan species which only casually overflows through some of the eastern Himalayan passes into the higher valleys of Sikkim and Chumbi. In the north-western Himalaya, from Kamaon to Kashmir, we find *M. horridula* replaced by a representative species, *M. aculeata*; in the eastern Himalaya *M. horridula* is, at slightly lower elevations, replaced by another representative species, *M. sinuata*. It now appears that in the corresponding area and at corresponding elevations in Szechuen and Yunnan *M. horridula* is similarly replaced by this third representative species, which is described below as *M. rudis*.

Taxonomy.

In arranging the species of *Meconopsis* the most satisfactory method is found to be that of grouping those species which agree in the greatest number of characters. This is not difficult, because, while we find in this as in other high alpine genera that the distribution of individual species is usually limited, we also find a complementary tendency to the occurrence, in distinct areas where the general conditions are similar, of representative species. The groups that it is necessary to recognize are somewhat unequal in number of component forms; these groups, rather than the actual species, probably represent the natural units of the genus. For further aggregation it is necessary to look for characters common to the various groups. Within the limits of the genus there is a wealth of striking differential morphological features and physiological peculiarities. Thus some species have stems, now simple now branched; others have none. Some have, others want a style; some have, others are without a disk. Some have papaveroid, others have sanguinarioid corollas; some have radiating divaricate, others have decurrent contiguous stigmatic lobes. Then some species are monocarpic, others are polycarpic; some have crowns that persist, others have crowns that die down during winter. Some flower in the same season as the seed, others flower in one year, or in two years, or occasionally after more than two years from seed. The temptation to employ as primary one or other of these salient differential characters is considerable. But further examination of all of them in the light of the actual characters of the natural groups shows us that the subdivision they effect is never complete. They traverse the evidence afforded by the actual groups and show us that in taxonomy there is no place for either morphological or physiological prepossessions. There is, however, one character,

at first sight trivial as compared with any of those enumerated, which can be used without violating the limits of any of the groups. This is derived from the nature of the hairs which compose the indumentum; these are sometimes simple, at others barbellate.

By the use of this character we are able to aggregate five of the natural groups into a section, *Eumeconopsis*, all the species of which have simple hairs; and into a second section, *Polychaetia*, the four remaining groups, all the species of which have barbellate hairs.

The five groups included in the section *Eumeconopsis* arrange themselves in two sub-sections, with the stems in one case slender and branching, in the other stouter, scapose and unbranched or altogether suppressed. The groups with slender stems that are or may be branched are the *Cambricae*, including only *M. cambrica*, perennial in duration, with no disk, a native of Europe; and the *Anomalae*, which are annuals, have the vertex of the capsule flattened and disk-like, and are natives of California. In these groups the indumentum is so sparingly present that the species are usually described as glabrous; we, however, always find hairs on the sepals of *M. cambrica*, and in the *Anomalae* we always find hairs on the margins of the leaves where they taper into or run along the sides of the petioles. The groups with unbranched stems or simple radical or pseudo-radical scapes are further easily sub-divided into the *Aculeatae*, which are prickly and may have either pinnately lobed or simple leaves; and into two unarmed groups, the *Primulinae*, monocarpic, with simple leaves, flowering one year from seed, and the *Bellae* with dissected leaves, a perennial habit, and only flowering after two or more years from seed. The four groups included in the section *Polychaetia* likewise arrange themselves in two sub-sections; one with the stems simple and scapose or altogether suppressed, the other with the stems branched. The groups with simple stems or no stems are two in number; the *Grandes* without a disk and with the stigmatic lobes radiating and divaricate, and the *Torquatae* with a true and well-developed disk and with the stigmatic lobes decurrent and contiguous. The two groups with branching stems are the *Robustae*, a very distinct group with stout much-branched stems with numerous flowers, monocarpic, with persistent crowns, flowering in the second year from seed; and the *Chelidonifoliae* with slender stems, few flowers, and a perennial habit. This last group consists of two species so remarkably alike that they can only be distinguished by their fruits; one of them has a stigma like that met with in the group *Grandes*, the other a stigma like that met with in all the groups except the *Grandes*. The *Chelidonifoliae* resemble, in general appearance, the group *Cambricae*, with which the writer at one time associated them. The affinity of the two groups outside the genus is, however, rather different; *M. cambrica* but for its capsule is a *Stylophorum*, the *Chelidonifoliae* but for their capsules are *Cathcartiae*.

The species of *Meconopsis*, with the exception of the forms from California which are annuals, have generally been described as perennials. It is not impossible that under natural oecological conditions a fair proportion of them may be so ; in cultivation, however, few of them are. Though none except the Californian forms are truly annual, most of them are monocarpic. In order to supplement his own knowledge and experience, the writer has consulted various friends who have had species of *Meconopsis* in cultivation, and is indebted for much of the information given below to Professor Bayley Balfour of Edinburgh, Mr. M. L. de Vilrmoin of Paris, Messrs. J. Veitch & Sons of Coombe Wood, and Mr. W. Irving of the Herbaceous Department at Kew. The evidence from herbarium material is rarely conclusive as regards species that have not yet been introduced to horticulture, and the only two as to which dried specimens appear to afford definite proof of a perennial habit are *M. chelidonifolia* and *M. Oliveriana*. In discussing the species seriatim it will be most convenient if they are dealt with group by group.

Cambricae. A single species, *M. cambrica*. Grows freely in most English gardens ; is always perennial ; as a rule self-sown seedlings appear in quantity.

Anomalae. Two forms, possibly not distinct species, *M. crassifolia* and *M. heterophylla*. Always hardy annuals, ripening seed readily in England.

Aculeatae. Two species of this group, *M. sinuata* and *M. rudis* are not yet known in cultivation ; this is also true of *M. horridula*. Of the remaining forms *M. aculeata* is very familiar. At Kew, plants of this species flower in about a year from time of germination, occasionally they take two years. They lose their crown of leaves during the winter months. Usually this species lasts only one year, dying after flowering ; at Kew, however, there has been one instance of a plant flowering two years in succession. At Edinburgh, though usually monocarpic, it is not always so, and Professor Balfour reports that several plants of this species have gone through three years of flowering. Self-sown seedlings frequently appear in the vicinity of the spot where a plant of *M. aculeata* has flowered. The other form of this group known in gardens is *M. racemosa*, Maxim. This is a biennial, flowering in a year from seed. It grows well and ripens seed freely. It is somewhat significant that this, which the writer takes to be only a condition, or at most a variety of *M. horridula*, should be well known, while true *M. horridula* is not known in cultivation. In the higher valleys of Sikkim, which the species, whereof both *M. horridula* and *M. racemosa* appear to be states, invades by crossing the inner passes, this is plentiful ; it does not, however, appear to occur below 14,000 feet or to the south of the outer passes and of the line of snowy peaks like Kinchinjanga, Chumiamo and Kinchinjhao, that mark the main axis of the Himalaya in this region. Below 14,000 feet and to the south of these peaks the species is sparingly replaced by *M. sinuata*, apparently a distinct though nearly related species which is represented at corresponding altitudes in the western Himalaya by *M. aculeata*, and in alpine Yunnan and Szechuen by *M. rudis*. To the north of these snowy peaks, and on the inner passes such as the Kongra-lama and the Tang-la, the form usually

met with is *M. horridula*; at or above 16,000 feet this is practically the only form present. To the north of the inner passes below 16,000 feet both forms occur side by side, and there is every transition between *M. horridula* proper with all the scapes simple, discrete, and radical; *M. horridula* still, but with some or all of the scapes agglutinated at the base; and *M. racemosa*, with all the flower disposed on a central several-flowered scape in a bractless raceme-like cyme. In specimens from the hills above Lhassa we sometimes find that the lowest and last-opening flower of this cyme is subtended by a leafy bract such as is associated with the lowest three-fourths to four-fifths of the flowers of *M. aculeata* and *M. sinuata*, and with the lowest half to two-thirds of the flowers of *M. rudis*. When we take into consideration the fact that the form distinguished by Maximowicz as *M. racemosa* occurs throughout central and eastern as well as southern Tibet, and is the only form that overflows into the high alpine valleys of Szechuen and Kansuh, while *M. horridula* is confined to southern Tibet and the high alpine valleys of Sikkim and Phari, it is reasonable to surmise that *M. horridula* may be no more than a somewhat reduced condition of a Tibetan species whereof *M. racemosa* is the usual state.

The evidence from the *Aculeatae*, incomplete though it be, is sufficient to show that the morphological character based on the presence or absence of a stem, though it has in the past been considered of sectional value, is not adequate to distinguish one form from another as species. It is also sufficient to show that the physiological features of a monocarpic or polycarpic habit, or of flowering in one year or two years from seed, do not always hold good in individual species.

Primulinae. Three species of this group, *M. Delavayi*, *M. lancifolia* and *M. primulina* are unknown in cultivation. The remaining species, *M. Henrici*, has recently been introduced to English gardens. Its behaviour at Coombe Wood in the hands of Messrs. Veitch and Sons, who have had much experience in growing species of *Meconopsis*, leads them to think that it cannot be perennial. It flowers in one year from seed.

Bellae. This group includes a single species, *M. bella*. Seeds of this sent to Europe by the writer from India have germinated at Kew, with Lieut.-Col. D. D. Cunningham at Torquay, with Mr. Bulley at Neston. They have also germinated at Geneva and elsewhere on the continent. It was stated in 1905 (Flora and Sylva, iii. 166, and Gard. Chron., ser. III. xxxvii. 370), that plants at Baden and at Edinburgh were likely to flower. Actual flowering was not, however, announced for either place, and the first record of its blossoming in cultivation has come this year (1906) from Edinburgh. In the case of this species two years have elapsed between seed and flower; there is little doubt that it is truly polycarpic. The crown of leaves persists during the winter. Unlike all other species so far known, this grows naturally on the faces of vertical cliffs; instead of flowering in spring or early summer, it flowers in late summer and autumn.

Grandes. This, the largest and one of the most natural of the groups of species in the genus, is characterized by the existence of a stigma like that of *Cathcartia*, section *Eucathcartia*. Striking, however, as this peculiarity is, it is not confined to the group; it recurs in the otherwise very different group *Chelidonifoliae*, a single member

of which has a stigma of the same character. This group also traverses the character to be derived from the stem, for two species, *M. integrifolia* and *M. grandis*, have distinct stems; the others have none. It traverses besides the character based on the presence or absence of a style; two species, *M. integrifolia* and *M. punicea*, have none; the others have a well-developed style. The group treats outstanding physiological features with equally scant ceremony. *M. punicea*, *M. quintuplinervia*, *M. simplicifolia*, and *M. pseudointegrifolia* all flower in one year from seed, all lose their crown of leaves during the intervening winter, and all die after flowering. *M. integrifolia*, too, has proved monocarpic with all those, and they are now numerous, who have grown it in Europe. At Kew this species flowers in twelve months from seed, loses its crown of leaves during the winter months, and dies after flowering. Both at Kew and at Coombe Wood it is found that plants a year old which fail to flower, die at the same time as plants of the same batch which have flowered. Seeds are found to ripen freely and germinate quickly if sown when ripe. They also germinate well if kept till the following spring. Messrs. Veitch & Sons find the best results are obtained by sowing in June and planting out when the seedlings are 2–2·5 in. high; plants so treated flower early in the summer following. A curious deviation from the experience at Kew and Coombe Wood has, however, been recently recorded by Mr. G. M. Sanders (Garden, lxx. 100), where seed of this species did not germinate till a year after sowing, and Mr. M. L. de Vilmorin has also experienced an equally interesting deviation with plants of *M. integrifolia* which, owing to a casual exigency, had to be grown in pots instead of being planted out. These did not flower in one year from seed and yet did not die. They lived through a second winter and flowered, as the species of the group *Robustae* do, in the second year from seed, dying after flowering. For this species it is found at Coombe Wood that full exposure is essential and that the plants improve if there are cold rough nights during the flowering stage. This experience, to those familiar with the climatic conditions of the Tibetan borderland, is not surprising. The plants flower well in open quarters but the best results are obtained in partial shade. *M. grandis*, the last species of this group, was introduced to European horticulture from India a number of years ago. The first to flower the plant in England was the late Mr. Thompson of Ipswich. It has since been flowered at Coombe Wood, at Neston, and at Edinburgh. At Kew this, like *M. bella*, has always perished in the seedling stage. At Coombe Wood it flowered poorly and did not prove perennial. At Neston it has proved polycarpic but has only been kept alive under protection. At Edinburgh, however, it has done well and has proved definitely polycarpic. Writing in August, 1906, Professor Balfour says: 'About a dozen plants which flowered this year are now forming their new crown-bud foliage. One old plant has flowered in at least a dozen successive years and is vigorous, with a group of daughter lateral shoots at the base.' At Edinburgh the crown leaves persist during winter. If only morphological characters be considered, it is difficult to separate this species from *M. simplicifolia*, from which it mainly differs by having a distinct scapose stem and by being rather larger in all its parts. Yet *M. simplicifolia*, like the other species of the group except *M. grandis*, is monocarpic and loses its crown of leaves during the winter that intervenes between seed and flower.

Torquatae. Of the two species in this group *M. torquata* is not yet known in cultivation; *M. discigera* has been introduced and there are young plants both at Kew and Edinburgh, probably also elsewhere. It promises, like *M. bella*, to be a species that may take several years between seed and flower; whether it is monocarpic or polycarpic cannot be predicted.

Robustae. The five species of this group appear all to behave alike. They take two years to reach the flowering stage; after flowering they die. In all, the rosette of crown-leaves persists during winter. In this group, therefore, the physiological features and morphological characters are clearly defined and distinctive to a greater degree than they are in most of the groups. At Kew the different species of the group do not behave uniformly; thus *M. napaulensis* and *M. Wallichii* seed freely, while *M. paniculata* seldom sets seeds. This seems to be the case with *M. robusta* also in most English gardens, and probably is so with *M. superba*. *M. napaulensis* and *M. Wallichii* come true to seed if grown separately; if grown together they readily cross.

Chelidonifoliae. This group consists of two undoubtedly perennial species so curiously alike as regards rootstocks, stems, foliage, and flowers, that they are only separable by means of their ripe capsules. Yet as regards the capsules they differ greatly, for *M. chelidonifolia* has an ovate capsule with a distinct style, and a stigma with decurrent contiguous lobes like those of every species except the species in the group *Grandes*, while *M. Oliveriana* has a sessile stigma with radiating divaricate lobes exactly as in *M. integrifolia* and *M. punicea*, or in *Cathcartia villosa*. The capsule, too, is in shape identical with that of *Cathcartia villosa*, differing only in opening by short apical pores instead of opening by complete separation of the valves from the placental ribs.

The conditions which obtain in English gardens are not always those most suitable for the development of the species of *Meconopsis*. This applies more particularly to the Himalayan species, some of which suffer so greatly from winter fogs and from moisture lodging in the crown that they die outright. It is possible to protect them to some extent by placing sheets of glass in a slanting position above the crowns.

As regards duration, the groups *Cambricae*, *Bellae*, *Chelidonifoliae* are perennial. The other groups are monocarpic as a rule, the *Anomalae* being indeed annual. But within the group *Aculeatae* we find that *M. aculeata* is sometimes, and within the group *Grandes* that *M. grandis* is, as a rule, polycarpic. Among the monocarpic groups we find that while as a rule, though this is not without its exceptions, the flower follows a year from seed and the leaves of the crown die during the winter which intervenes, in the group *Robustae* the plants do not flower till the second year from seed, and the leaves of the crown persist during the two winters which intervene. But the question of duration can hardly be said to be settled for the genus by experience in horticulture under conditions admittedly unlike those to which the plants are naturally subjected. When it is seen that in the case of two, *M. aculeata* and *M. grandis*, a species may on occasion be either

monocarpic or polycarpic, it is permissible to inquire whether this habit-character is necessarily inherent. It may be conditioned by the environment, and be an accidental, not an essential feature.

As regards habit, as apart from duration, the species of *Meconopsis* fall into three main series. The first of these includes the species with slender non-scapose, sparingly branched, leafy stems. In facies the species of this series agree well. As regards duration they vary, for the series includes the only annual group the *Anomalae*, and two of the definitely perennial groups the *Cambricae* and the *Chelidonifoliae*. This series includes the species that are outliers from the main body of the genus, the Californian *Anomalae* and the European *Cambricae*; it also includes the only group belonging to the main body of the genus, the *Chelidonifoliae*, of which one member (*M. Oliveriana*) extends to central China. The second main series includes those species with stout non-scapose, much-branched, leafy stems. It corresponds to a single group, the *Robustae*, the members of which are monocarpic, flower in the second year from seed, and have, during winter, persistent leafy crowns. The third series includes those species with scapose unbranched stems or with no stems at all. As a rule the species are monocarpic, flower in the first year from seed, and have non-persistent leafy crowns. This series is, however, less uniform than the other two series, for there are some exceptions to the general rule. Thus *M. bella*, the only species of the group *Bellae*, and *M. grandis*, one of the species of the group *Grandes*, are uniformly perennial like the *Cambricae* and the *Chelidonifoliae* of the first series, and have persistent crowns like the *Robustae* of the second series. Among the *Aculeatae* too, *M. aculeata* is occasionally polycarpic. *M. bella*, besides being polycarpic and having persistent leafy crowns, differs from other species of the genus in sometimes not flowering till after several years from seed. This appears also to be probably the case with *M. discigera* of the group *Torquatae*, but this group is as yet inadequately known from the cultural point of view.

Distribution.

The distribution of the various species of *Meconopsis*, so far at least as our knowledge at present goes, is very local. This is in keeping with our knowledge of the species of other Alpine genera. The species at all widely spread are *M. cambrica*, which extends from the Pyrenees to Britain; *M. horridula* which occurs throughout the greater part of Tibet, and extends through some of the passes into the highest valleys of the eastern Himalaya and western China; *M. aculeata*, which extends along the north-western Himalaya from Kashmir to Kumaon; *M. simplicifolia*, which extends from Nepal to Chumbi, and crosses the passes into southern Tibet; *M. paniculata*, which extends from Nepal to Bhutan; *M. Wallichii*, which extends from Sikkim to Chumbi and reappears in Szechuen; and

M. integrifolia, which extends from Yunnan to Kansuh and passes into central Tibet. In the subjoined table the facts of distribution are more succinctly shown.

GEOGRAPHICAL DISTRIBUTION OF THE SPECIES OF *MECONOPSIS*.

Species.	W. Europe.	Himalaya.						Tibet.			China.				California.
		Kashmir.	Kumaon.	Nepal.	Sikkim.	Chumbi.	Bhutan.	S. Tibet.	C. Tibet.	N. Tibet.	Yunnan.	Szechuen.	Kansuh.	Hupeh.	
Meconopsis cambrica	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–
,, *heterophylla*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×
,, *crassifolia*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	×
,, *aculeata*	–	×	×	–	–	–	–	–	–	–	–	–	–	–	–
,, *sinuata*	–	–	–	–	×	–	×	–	–	–	–	–	–	–	–
,, *rudis*	–	–	–	–	–	–	–	–	–	–	×	×	–	–	–
,, *horridula*	–	–	–	–	×	×	–	×	×	×	–	×	×	–	–
,, *lancifolia*	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–
,, *Henrici*	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–
,, *primulina*	–	–	–	–	–	×	×	–	–	–	–	–	–	–	–
,, *Delavayi*	–	–	–	–	–	–	–	–	–	–	×	–	–	–	–
,, *bella*	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
,, *integrifolia*	–	–	–	–	–	–	–	–	×	–	×	×	×	–	–
,, *pseudointegrifolia*	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–
,, *grandis*	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
,, *simplicifolia*	–	–	–	×	×	×	×	×	–	–	–	–	–	–	–
,, *quintuplinervia*	–	–	–	–	–	–	–	–	–	×	–	–	×	–	–
,, *punicea*	–	–	–	–	–	–	–	–	–	×	–	×	–	–	–
,, *torquata*	–	–	–	–	–	–	–	×	–	–	–	–	–	–	–
,, *discigera*	–	–	–	–	×	–	–	–	–	–	–	–	–	–	–
,, *superba*	–	–	–	–	–	–	×	–	–	–	–	–	–	–	–
,, *paniculata*	–	–	–	×	×	×	×	–	–	–	–	–	–	–	–
,, *robusta*	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–
,, *napaulensis*	–	–	–	×	×	–	–	–	–	–	–	–	–	–	–
,, *Wallichii*	–	–	–	–	×	×	×	–	–	–	–	×	–	–	–
,, *chelidonifolia*	–	–	–	–	–	–	–	–	–	–	–	×	–	–	–
,, *Oliveriana*	–	–	–	–	–	–	–	–	–	–	–	×	–	×	–
	1	1	2	3	9	5	6	4	2	3	4	8	3	1	2

Meconopsis is very largely an alpine genus, there being only three species to which the term cannot be applied. These are the three that, by their distribution, are geographically furthest removed from the main body of the genus, viz.:—the West European *M. cambrica*, and the Californian *M. heterophylla* and *M. crassifolia*. These three are not even sub-alpine; they do not occur above 2,500 feet.

Of the Himalo-Chinese and Tibetan species, on the other hand, none come below 7,500 feet, and the only ones that ever appear to deserve being considered sub-alpine are *M. robusta* in Kumaon, *M. Oliveriana* in Hupeh, and *M. quintuplinervia* in Kansuh. All three species named, however, also reach truly alpine altitudes. The great bulk of the genus is to be found only at or above 10,000 feet; few of them indeed occur quite so low

down as this, 11,000-13,000 feet being the usual range. Three of the species go as high as 16,000 feet, one of these, *M. horridula*, goes beyond 17,500 feet.

While, however, *Meconopsis* is essentially an alpine genus, it differs from many alpine genera in not being at the same time an Arctic one. It is not only confined to the northern hemisphere, but is restricted to a curiously narrow belt in that hemisphere. Of the twenty-seven species no fewer than twenty-two are confined to the zone between 25° and 30°

ALTITUDINAL AND LATITUDINAL DISTRIBUTION OF THE SPECIES OF *MECONOPSIS*.

Species.	Altitude in feet above sea-level.								Latitude north of the Equator.					
	0–2,500	2,500–5,000	5,000–7,500	7,500–10,000	10,000–12,500	12,500–15,000	15,000–17,500	Over 17,500	25°–30°	30°–35°	35°–40°	40°–45°	45°–50°	50°–55°
Meconopsis cambrica	×	–	–	–	–	–	–	–	–	–	–	×	×	×
„ *heterophylla*	×	–	–	–	–	–	–	–	–	–	×	–	–	–
„ *crassifolia*	×	–	–	–	–	–	–	–	–	–	×	–	–	–
„ *aculeata*	–	–	–	–	×	×	–	–	–	×	–	–	–	–
„ *sinuata*	–	–	–	–	×	×	–	–	×	–	–	–	–	–
„ *rudis*	–	–	–	–	–	×	–	–	×	–	–	–	–	–
„ *horridula*	–	–	–	–	–	×	×	×	×	×	×	–	–	–
„ *lancifolia*	–	–	–	–	×	×	–	–	×	–	–	–	–	–
„ *Henrici*	–	–	–	–	×	×	–	–	×	–	–	–	–	–
„ *primulina*	–	–	–	–	×	×	–	–	×	–	–	–	–	–
„ *Delavayi*	–	–	–	–	×	×	–	–	×	–	–	–	–	–
„ *bella*	–	–	–	–	×	×	–	–	×	–	–	–	–	–
„ *integrifolia*	–	–	–	–	–	×	×	–	×	×	×	–	–	–
„ *pseudointegrifolia*	–	–	–	–	–	×	–	–	×	–	–	–	–	–
„ *grandis*	–	–	–	–	×	–	–	–	×	–	–	–	–	–
„ *simplicifolia*	–	–	–	–	×	×	×	–	×	–	–	–	–	–
„ *quintuplinervia*	–	–	–	×	×	–	–	–	–	–	×	–	–	–
„ *punicea*	–	–	–	–	×	–	–	–	×	×	–	–	–	–
„ *torquata*	–	–	–	–	×	–	–	–	×	–	–	–	–	–
„ *discigera*	–	–	–	–	×	–	–	–	×	–	–	–	–	–
„ *superba*	–	–	–	–	×	–	–	–	×	–	–	–	–	–
„ *paniculata*	–	–	–	–	×	–	–	–	×	–	–	–	–	–
„ *robusta*	–	–	–	×	×	–	–	–	×	×	–	–	–	–
„ *napaulensis*	–	–	–	–	×	–	–	–	×	–	–	–	–	–
„ *Wallichii*	–	–	–	–	×	–	–	–	×	–	–	–	–	–
„ *chelidonifolia*	–	–	–	–	×	×	–	–	×	–	–	–	–	–
„ *Oliveriana*	–	–	–	×	×	–	–	–	×	×	–	–	–	–
	3	0	0	3	20	13	3	1	22	6	5	1	1	1

lat. N.; only six are found between 30° and 35° lat. N.; and of the Asiatic species only three extend into the zone between 35° and 40° lat. N. Of these only two, *M. horridula* and *M. integrifolia*, appear to occur in all three zones.

The Californian species are confined to the 35° to 40° lat. N. zone, so that they do not extend the genus further to the north than do the Asiatic species. The European species *M. cambrica*, however, is exceptional in the genus in this as in other distributional characteristics, for it extends through more than 12° of latitude, and occurs in the zones 40° to 45°, 45° to 50°, and 50° to 55°.

The tables foregoing show the facts of distribution as regards altitude and latitude in a more compact form.

Taken as a whole the facts of distribution as regards *Meconopsis* seem to indicate that, however advisable it may be to treat the flora of central and eastern China as distinct from that of India or even of Indo-China, the alpine flora of western China is essentially the same as that of the Himalayas.

It is highly probable that our acquaintance with this genus is as yet far from complete. Our knowledge of the high Himalayan valleys is doubtless fairly adequate so far as the region from Kashmir to Kumaon is concerned, and it is hardly to be anticipated that any species of *Meconopsis* remains undiscovered between lon. 73° and lon. 82° E. But as regards Nepal we know nothing of the high alpine vegetation save within a narrow segment near the 85th meridian, which has been investigated by Wallich and Scully. Thanks to the energy of Sir J. D. Hooker, and to the efforts of Sir G. King, a small section of the eastern Himalaya between the 88th and 89th meridians has been as fully explored as any portion of the north-west Himalaya, with the result that this narrow strip has yielded no fewer than eleven species, of which seven, so far as we know, are peculiar to this limited belt. Some of these seven, like *M. grandis*, *M. discigera*, and *M. bella*, have only been found in the extreme west of the belt, and in all likelihood extend westward into unexplored Nepal; others, like *M. superba* and *M. primulina*, have only been found in the extreme east of the same narrow strip, and equally probably will be found to extend eastward into Bhutan. Between the 99th and the 105th meridians, from 25° to 40° lat. N., we have a belt of country which, thanks to the efforts of French missionaries in the south and centre, and of Russian explorers in the centre and north, supplemented as regards the centre by those of English travellers, has been tolerably investigated. This belt has also yielded eleven species, of which again seven, so far as we know, are peculiar. Of the alpine vegetation of the Himalayan region between the 89th and the 99th meridians we know practically nothing; and of the Tibetan region behind and to the north we only know that, out of four species of *Meconopsis* which it has so far yielded, two, *M. torquata* from the Kyi-chu valley and *M. pseudointegrifolia* from the Ra-chu valley, are distinct from any species recorded from either of the belts of relatively well-explored country alluded to. If all the circumstances are considered we seem entitled to anticipate that the

conditions in the Himalayan country still to be explored are similar to those known to prevail in the portions as to which we already possess some information. If this should prove to be really the case we may expect to find that in the genus *Meconopsis* there are possibly some forty distinct forms.

PROPERTIES.

The properties of the species of *Meconopsis* are obscure. According to Don the root of *M. paniculata* is poisonous; the statement must obviously have been derived from a note by Wallich, and no doubt represents what Wallich was told by native collectors in Nepal. According to Hooker and Thomson, the natives of Sikkim are of the same belief as regards *M. Wallichii*, and according to Stewart the natives of Chamba think the same of *M. aculeata*. O'Shaughnessy, however, found that *M. aculeata* did not have much effect on lower animals, and although Honigberger has included this species among his officinal plants of Kashmir, he only remarks that it is 'said to be' narcotic, and indicates its use in cases of 'troubled sight.' Dymock, Warden, and Hooper have examined the roots of *M. Wallichii* chemically, but impute to it neither deleterious nor useful properties. In the 'Dictionary of the Economic Products of India,' v. 197, 198 (1891), Watt has been unable to add any further information on the subject. Watt's remarks as to the medicinal properties imputed to *M. nipalensis* belong, it should be noted, to *M. aculeata*. They are derived from Honigberger and refer to Kashmir. In the first place neither the true *M. napaulensis* nor *M. paniculata* (the plant which Watt terms *M. nipalensis*) occurs in Kashmir; moreover, Honigberger gives a figure of the plant intended by him as *M. nepalensis*. This figure is a good representation of the spiny, blue Poppy of Kashmir, *M. aculeata*.

MECONOPSIS, VIG.

Hist. Pav. Diss., 20 (1814); DC. Syst., ii. 86, *Stylophoro* excl. (1821); Bernh., Linnaea, viii. 462 (1833); Endl., Gen., 836 (1841); Benth. & Hook. f., Gen. Pl., i. 52 (1862); Baill., Hist. des Plantes, iii. 140 (1872); Prantl & Kundig, Nat. Pflanzenfam., iii. 2, 141 (1889).

Sepala 2. Petala nunc 4, nunc 5–9. Stamina ∞. Ovarii placentae 4–∞ nerviformes vel plus minusve intrusae; stylus saepissime distinctus, raro obsoletus; stigmatis clavati vel depresso-dilatati lobi decurrentes contigui vel radiantes divaricati placentis oppositi. Capsula ovoidea, oblonga vel rarissime anguste cylindracea vertice saepius in stylum sensim attenuata, aliquando in discum astigmaticum circa basin styli explanata, valvis brevibus placentas styloque persistentes nudantibus dehiscens. Semina scrobiculata raphe cristata vel nuda.—Herbae saepissime monocarpicae nonnunquam tamen perennantes succo flavo. Folia integra vel

lobata vel rarissime dissecta. Flores saepius longe pedunculati singuli vel in cymas racemiformes, vel raro paniculatas rarissime umbelliformes dispositi, speciosi, alabastris nutantibus.

Species adhuc recognitae 27 quarum 1 in Europa occidentali, 2 in America boreali-occidentali, 10 in China, 2 in Tibetia, 12 in Himalaya crescunt; forsan tamen ad 20 reducendae.

Genus in sectiones 2, sectiones iterum in greges naturales 9 commode dividuntur, scil.:—

§ **Eumeconopsis.** Glabrae vel aculeis setis pilisve simplicibus plus minusve obsitae.

Caules graciles ramosi; folia caulina pinnatipartita radicalia aequantia vel superantia:—

Capsula vertice sensim in stylum attenuata; perennantes ¶ *Cambricae.*

Capsula vertice quasi in discum astigmaticum explanata; annuae ¶ *Anomalae.*

Caules scapiformes simplices, vel caules 0; folia caulina radicalibus minora vel 0:—

Plantae aculeis rigidis pungentibus ubique armatae ¶ *Aculeatae.*

Plantae glabrae vel sparse hirsutae setosaeve, inermes:—

Folia integra; plantae monocarpicae ¶ *Primulinae.*

Folia dissecta; plantae polycarpicae ¶ *Bellae.*

§§ **Polychaetia.** Setis pilisve barbellatis ubique plus minusve indutae.

Caules scapiformes simplices, vel caules 0; folia plerumque vel omnia radicalia subintegra:—

Capsula haud discigera; stigma depresso-dilatatum lobis radiantibus divaricatis ¶ *Grandes.*

Capsula vertice in discum lobatum astigmaticum explanata; stigma clavatum lobis decurrentibus contiguis ¶ *Torquatae.*

Caules ramosi; folia varie lobata vel pinnatifida, caulina numerosa:—

Caules robusti; flores sat numerosi; plantae monocarpicae ¶ *Robustae.*

Caules graciles; flores pauci; plantae polycarpicae ¶ *Chelidonifoliae.*

Clavis specierum.

Setis vel pilis vel aculeis simplicibus obsitae vel fere omnino glabrae:—

Caules graciles ramosi; folia caulina pinnatipartita radicalia aequantia vel superantia:—

Capsula vertice sensim in stylum attenuata; flores concolores lutei; perennans 1. *cambrica.*

Capsula vertice quasi in discum astigmaticum explanata; flores lateritii purpureo-ocellati; annuae:—

Folia caulina internodis breviora; capsula angusta valvis 4–5 2. *heterophylla.*

Folia caulina internodis longiora; capsula lata valvis 6–10 3. *crassifolia.*

Caules scapiformes simplices, vel caules 0; folia caulina radicalibus minora vel 0; flores coerulei:—

Plantae aculeis pallidis rigidis pungentibus ubique armatae:—

Folia distincte lobata; petala 4; torus vix incrassatus:—

Folia pinnatipartita; capsula ovata — 4. *aculeata.*

Folia sinuato-lobata; capsula elongato-obconica — 5. *sinuata.*

Folia subintegra; petala saepissime 5–8; torus sub capsulam late amplius:—

Folia caulina a basi ad medium cymae usque evoluta — 6. *rudis.*

Folia caulina 0:—

Flores in scapis 1-floris interdum basi coalitis singuli — 7. *horridula.*

Flores in cymas ebracteatas racemiformes dispositi — 7 b. *horridula*, var. *racemosa.*

Plantae inermes setis pilisve simplicibus indutae, vel fere glabrae:—

Folia integra vel subintegra; plantae monocarpicae:—

Folia lanceolata:—

Flores in cymas ebracteatas racemiformes dispositi; petala 4 — 8. *lancifolia.*

Flores in scapis radicalibus singuli raro bini; petala 5–8:—

Capsula statim in stylum abeuns; stigma integrum — 9. *Henrici.*

Capsula circa basin styli papillis obsita; stigma 2-lobum — 10. *primulina.*

Folia spathulato-oblonga; petala 5–8, scapis 1-floris — 11. *Delavayi.*

Folia pinnatisecta; flores in scapis radicalibus singuli; petala saepissime 4; planta polycarpica — 12. *bella.*

Setis pilisve barbellatis ubique plus minusve indutae:—

Caules scapiformes simplices, vel caules 0; folia plerumque vel omnia radicalia subintegra:—

Capsula haud discigera; stigma depresso-dilatatum, lobis radiantibus divaricatis:—

Flores lutei; petala 5–8:—

Caulis scapiformis; flores in cymas subumbelliformes 3–7-floras dispositi; stylus 0 — 13. *integrifolia.*

Caulis 0; flores in scapis radicalibus singuli; stylus elongatus — 14. *pseudointegrifolia.*

Flores coerulei, purpurei vel punicei:—

Caulis scapiformis; flores in cymas subumbelliformes 3-floras 1–2 inferioribus sparsis interdum adiectis dispositi; petala 5–9, stylus elongatus — 15. *grandis.*

Caulis 0; flores in scapis radicalibus singuli:—

Stylus elongatus; flores coerulei vel purpurei:—

Petala 5–8; capsula sparse setosa — 16. *simplicifolia.*

Petala 4; capsula dense setosa — 17. *quintuplinervia.*

Stylus 0; flores punicei; petala saepissime 4, raro 8–9 — 18. *punicea.*

Capsula vertice in discum lobatum astigmaticum glabrum explanata; caulis scapiformis; flores in cymas multifloras subspicatas dispositi:—
Discus lobis integris; stylus perbrevis 19. *torquata.*
Discus lobis incisis; stylus elongatus 20. *discigera.*
Caules ramosi; folia radicalia distincte lobata vel pinnatifida; caulina numerosa:—
Caules crassi; flores plurimi saepissime paniculati; plantae monocarpicae:—
Capsula ovata 8–11-valvata; stylus brevis basi distincte incrassatus:—
Flores albi; folia caulina grosse dentata 21. *superba.*
Flores lutei:—
Folia caulina grosse dentata 22. *paniculata.*
Folia caulina pinnatifida 23. *robusta.*
Capsula oblonga 5–7-valvata; stylus elongatus; folia caulina pinnatifida:—
Flores fusco-purpurei 24. *napaulensis.*
Flores coerulei 25. *Wallichii.*
Caules graciles; flores pauci laxe cymosi; plantae polycarpicae:—
Capsula ovata; stylus elongatus; stigma clavatum 26. *chelidonifolia.*
Capsula anguste cylindracea; stylus 0; stigma depresso-dilatatum 27. *Oliveriana.*

§ I. EUMECONOPSIS. Herbae nonnunquam fere glabrae, sed saepius pilis, setis aculeisve simplicibus plus minusve obsitae; capsula saepissime sensim in stylum attenuata, raro vertice circa basin styli quasi in discum astigmaticum explanata; stigma clavatum lobis decurrentibus contiguis.—Herbae saepius monocarpicae, nonnunquam equidem annuae; paucae tamen perennantes. *Meconopsis* § *Meconopsis*, DC. Syst. Veg., ii. 86 (1821); Prodr., i. 120 (1824).

¶ 1. *Cambricae*, Prain. Inermes; perennantes; caules elongati ramosi foliosi, folia pinnatifida glabra; sepala parce pilosa; flores lutei petalis 4; styli distincti; capsula glabra sensim in stylum attenuata. *Chelidonifoliae*, Prain, Journ. As. Soc. Beng., lxiv. 2. 313 (1895) partim.

1. **Meconopsis cambrica**, Vig. Rhizoma glabrum; folia ovato-lanceolata, segmentis ovato-lanceolatis, lobis acutis, caulibusque glabra; sepala hirsuta; capsula ovata, stylo distincto. Vig., Hist. Pav. Diss., 48, fig. 3 (1814); DC. Fl. Fr., ed. 3, v. 586 (1815); Syst. Veg., ii. 87 (1821); Mem. Soc. Phys. Nat. Gen., i. t. 2, fig. 12 (1821); Prodr., i. 120 (1824); Lindl., Syn. Brit. Fl., ed. 1, 17 (1829); Hook., Brit. Fl., ed. 1, 256 (1830); Baxt., Brit. Bot., i. t. 54 (1834); Mackay, Fl. Hibern., 14 (1836); Bab., Man. Brit. Bot., ed. 1, 12 (1843); ed. 9, 19 (1904); Deakin, Florigr. Brit., ii. 754, t. 856 (1845); Syme, Eng. Bot., ed. 3, t. 63 (1863); Moore and More, Cybele Hibern., ed. 1, 13 (1866); Hook. f., Stud. Fl. 16 (1870); Willk. & Lange, Fl. Hispan., iii. 873 (1880); H. C. Wats., Topog. Bot., ed. 2, 23 (1883); Colmeiro, Enum. Pl. Hispan. Lusit., i. 101 (1885); Coste, Fl. Fr., i. 61 (1901); Flora and Sylva, iii. 82 (1905). *Argemone Cambro-Britanica lutea*, Parkins., Theatr. Bot., 369, 370 (1640). *A. cambrica*,

Desp., Dict. Sci. Nat., ii. 481 (1816); Nouv., Dict. Hist. Nat., ii. 462 (1816). *Papaver cambricum perenne flore sulphureo*, Dill., Hort. Elth., 300, t. 223 (1732). *P. cambricum*, Linn., Sp. Pl., ed. 1, 508 (1753); Hill, Herb. Brit., ii. 235, t. 154 (1770); Sowerby & Sm., Eng. Bot., ed. 1, t. 66 (1790); Sm., Fl. Brit., i. 568 (1800); Poir., Encyc. Meth., v. 117 (1804); DC., Fl. Fr., ed. 3, iv. 633 (1805); Hook., Fl. Scot., i. 168 (1821). *Cerastites cambrica*, S. F. Gray, Nat. Arr. Brit. Pl., ii. 704 (1821). *Stylophorum cambricum*, Spreng., Syst., ii. 570 (1825); Steud., Nomencl., ed. 2. 650 (1841).

EUROPA OCCIDENTALIS. In sepibus et dumetis umbrosis a Pyrenaeis ad Hiberniam, Cambriam Cumbriamque usque; nunquam supra 2000 p.s.m.

The well-known Welsh Poppy, familiar as a wild plant in western France and England and in Ireland: often in gardens and occasionally naturalized in parts of Britain other than those in which it is a native species. Polycarpic. Occasionally in cultivated plants there are more than four petals.

As a group the *Cambricae*, which includes a single form, is very natural. In habit it agrees with only one other group, the *Chelidonifoliae*, in which at one time the writer proposed to include *M. cambrica*. Among the Papaveraceae as a whole this group most resembles the section *Stylophorum* of the genus *Chelidonium*; so close is the affinity that De Candolle and others have treated *Stylophorum* and *M. cambrica* as congeneric.

¶ 2. *Anomalae*, Prain, Journ. As. Soc. Beng., lxiv. 2. 313 (1895). Inermes; annuae; caules elongati ramosi foliosi; folia irregulariter pinnatipartita glabra; flores lateritii vel aurantiaci purpureo-ocellati petalis 4; styli distincti; capsula glabra circa basin styli quasi in discum astigmaticum explanata.

2. **Meconopsis heterophylla**, Benth. Caules apicem versus laxe ramosi; folia pauca herbacea radicalia evanida caulina internodis breviora; capsula anguste turbinata saepissime valvis 4–5 quadrante summo aperta (Pl. XXIV, Fig. 9). Benth. in Trans. Hort. Soc., ser. II, i. 408 (1835); Torr. & Gray, Fl. N. Amer., i. 61 (1838); Hook. & Arn., Bot. Beechey Voy., 320 (1840); Hook., Ic. Pl., t. 732 (1845); Torr. in Pacif. Rail. Rep., iv. 64 (1857); Bot. U. S. Mex. Bound. Surv., 31 (1858); Bot. Calif., i. 22 (1888); Rattan, Pop. Calif. Fl., ed. 8, 21 (1888); Pars. & Buck, Wild Fl. Calif., 129 (1897); Hook., Bot. Mag., t. 7636 (1899); Gard. Chron., ser. III, xxix. 412, fig. 55 (1901); Abrams, Fl. Los Ang., 162 (1904); Flora and Sylva, iii. 82 (1905). *Stylophorum heterophyllum*, Steud., Nomencl., ed. 2, ii. 650 (1841). *Papaver heterophyllum*, Greene, Pittonia, i. 168 (1888); Fl. Francisc., 281 (1892); Man. Bot. San Francisc. Bay, 9 (1894); Jepson, Fl. West Mid. Calif., 209 (1901).

AMERICA BOREALI-OCCIDENTALIS. California; in cultis, an semper?

Apparently an agrestal state of the next form.

3. **Meconopsis crassifolia,** Benth. Caules a basi ramosi ; folia satis numerosa carnosula radicalia subpersistentia caulina internodis longiora ; capsula late turbinata saepissime valvis 6 vel pluribus apice tantum brevissime aperta (Pl. XXIV, Fig. 10). Benth. in Trans. Hort. Soc., ser. II, i. 408 (1835); Torr. & Gray, Fl. N. Amer., i. 61 (1838); Hook. & Arn., Bot. Beechey Voy., 320 (1840). *Stylophorum crassifolium*, Steud., Nomencl., ed. 2, ii. 650 (1841). *Papaver crassifolium*, Greene, Man. Bot. San Francisc. Bay, 9 (1894). *P. heterophyllum*, var. *crassifolium*, Jepson, Fl. West Mid. Calif., 209 (1901).

AMERICA BOREALI-OCCIDENTALIS. California ; in pratis, dumetis agrisque.

Doubtfully separable from the preceding.

The *Anomalae* constitute a natural group, distinguished from all other groups in being not only monocarpic but annual, and in having the petals marked by a dark basal blotch ; in the other known species the petals are concolorous. The foliage is more deeply divided than in any group except the *Bellae*. These two groups, the *Bellae* and the *Anomalae*, further agree in that the apices of the valves by which the capsules dehisce do not quite extend to the base of the style, and so leave the vertex of the capsule solid. In the *Bellae* the solid portion surrounding the base of the style is convex and is not very extensive. In the *Anomalae*, however, this solid part of the capsule is as wide as the capsule itself, is almost flat, and resembles the disk of a true *Papaver* except in being astigmatic. This flattened vertex, however, is hardly a disk in the sense of the term as used in the case of a *Papaver* like *P. somniferum* or *P. dubium*, because the margin ends at, but does not project beyond, the margins of the valves.

The question whether there are more species than one in the group *Anomalae* has been often discussed but has not been satisfactorily settled. An examination of the material in the herbarium at Kew shows that there are certainly two forms corresponding more or less closely to the types of Bentham's two species. The remarks of such competent authorities as Greene and Jepson indicate that in the field also two forms are more or less distinguishable. But how far the forms distinguished by Greene and Jepson correspond to the species defined by Bentham, and which form as recognized in the field in California corresponds with either name given by Bentham, is not so clear as could be wished. The difficulty was explained by Greene in 1891 (Flor. Francisc. 281) at which time he was doubtful whether his two forms represented more than states of one species differing in facies in consequence of their environment. By 1894 Greene had become satisfied (Bot. San Francisc. Bay, 9) that, of the two forms recognized by him, the one from wooded slopes corresponds to Bentham's *M. heterophylla*, the one from dry fields to *M. crassifolia*. Jepson in 1901 (Flor. West Mid. Calif. 209) has followed Greene's discrimination of 1894, though he treats the two forms as merely varieties of one species. Unfortunately with the specimens at Kew which agree with the type of *M. heterophylla* we have in no instance any note as to habitat, while of the specimens that agree with *M. crassifolia* some are from grassy banks, some from shaded cañons, some from

fields of growing grain. At the same time some of the specimens at Kew which accord well with *M. crassifolia* have been so named by competent Californian botanists; others, however, have been named *M. heterophylla*, with which they do not so well agree. The writer is, therefore, led to suspect that within what must in the herbarium be treated as *M. crassifolia* there may be two forms or conditions recognizable in the field, and that the true *M. heterophylla* is either a further segregate from one of these forms or is not accounted for in recent Californian botanical literature. This last possibility is suggested by the remark made by Greene in 1891, that he had been unable to find in California a plant with capsules like those figured by Hooker (Ic. Plant., t. 732). Yet this figure represents very accurately a plant from California which the writer agrees with Sir W. Hooker in referring to the true *M. heterophylla*, Benth. Under the circumstances all that it is possible to do is to give, as has been done above, the salient characters of Bentham's two plants and to leave them for the moment as Bentham left them. The true relationship of the two must be settled in the field, and a final decision can only be come to by our colleagues in California. It may, however, be observed that while Greene has decided that there are two species, Jepson has considered Greene's two species as no more than varieties of one, and Rattan has concluded that there is but one Californian *Meconopsis*. Sir J. Hooker, after examining the material at Kew, which includes Bentham's types of *M. heterophylla* and of *M. crassifolia*, has expressed the same opinion as Rattan, and the writer is personally inclined to adopt the view of Rattan and Hooker. Indeed, if one could judge from herbarium specimens only, the natural conclusion would seem to be that in Bentham's *M. crassifolia* we see the normal state of this solitary species, whereas in *M. heterophylla* we have an agrestal condition of the same plant with quickly disappearing radical leaves, elongated internodes, a weak, slender, often straggling, stem and smaller flowers and fruits, owing to the plant having been 'drawn up' among tall grass or grain. This conclusion is, however, partially traversed by the experience of Greene and Jepson as recorded in their respective works and by the experience of various collectors as recorded in their field-notes.

One difficulty in connexion with the settlement of the question is that there are no ripe capsules on the original specimens on which Bentham based *M. heterophylla* and *M. crassifolia*. The drawing of the fruit of the former plant (Pl. XXIV, Fig. 9) is taken from a specimen identified by Sir W. Hooker with *M. heterophylla*, Benth. There is hardly room for doubt that this identification is correct. The drawing of the fruit of the latter (Pl. XXIV, Fig. 10) is from a specimen collected by C. F. Baker, and identified by Greene with Bentham's *M. crassifolia*; here again the identification seems certainly accurate.

In European gardens, so far as can be ascertained, only one species of *Meconopsis* from California can be recognized.

¶ 3. *Aculeatae*, Prain, Journ. As. Soc. Beng., lxiv. 2. 313 (1895). Armatae; saepius monocarpicae aliquando tamen perennantes; caules saepissime evoluti simplices scapiformes raro 0; flores coerulei petalis nunc 4, nunc 5–8; styli distincti; capsula echinata sensim in stylum attenuata.

4. **Meconopsis aculeata,** Royle. Folia sparse aculeata lineari-oblonga lanceolatave irregulariter pinnatifido-lobata lobis varie lobulatis; flores in cymas racemiformes dispositi, pedicellis fere omnibus bracteatis; petala 4; capsula ovata stylo duplo longior; torus vix ampliatus. Royle, Ill. Him., 67, t. 15 (1839); Walp., Rep., i. 110 (1842); O'Shaughnessy, Beng. Dispens., 184 (1842); Beng. Pharm., 5 (1844); Hook. f. & Thoms., Fl. Ind., 253 (1855); Walp., Ann., iv. 171 (1857); Klotzsch, Reis. Pr. Waldem., 129 (1862); Hook., Bot. Mag., t. 5456 (1864); Stewart, Panjab Plants, 9 (1869); Hook. f. & Thoms., Fl. Brit. Ind., i. 118 (1872); Prain, Journ. As. Soc. Beng., lxiv. 2. 314 (1895); Collett, Flor. Siml., 23 (1902); Flora and Sylva, iii. 82 (1905); Strachey, Pl. Kumaon, 8 (1906). *M. Gulielmi-Waldemari*, Klotzsch, Reis. Pr. Waldem., 129, t. 36 (1862). *M. napaulensis*, Jacquem. ex Prain, Journ. As. Soc. Beng., lxiv. 2. 314 (1895); Falc. ex Prain, *loc. cit.* (1895). *M. nepalensis*, Honigberger, Thirty-five Years in the East, ii. t. 15 (1852). *Stylophorum nepalense*, Honigberger, Thirty-five Years in the East, ii. 352 (1852).

HIMALAYA OCCIDENTALIS. A Kumaon ad Kashmir usque; in pratis alpinis, 10–15,000 p. s. m.

Representative in the North-West Himalaya of the Tibetan *M. horridula*. Differs from *M. rudis* and *M. horridula* in the lobed leaves and narrow torus, from *M. sinuata* in the shorter capsule. Well known in cultivation and usually monocarpic. At Edinburgh plants have, however, flowered in three successive seasons; at Kew one plant has flowered in two successive seasons.

5. **Meconopsis sinuata,** Prain. Folia sparse aculeata lineari-oblonga lanceolatave margine irregulariter lobata sinuatave lobis integris; flores in cymas racemiformes dispositi, pedicellis fere omnibus bracteatis; petala 4; capsula anguste obconica stylo 5-plo longior; torus vix ampliatus. Prain, Journ. As. Soc. Beng., lxiv. 2. 314 (1895); Ann. Roy. Bot. Gard. Calcutta, ix. 1. 5. t. 6 (1901).

HIMALAYA ORIENTALIS. In Sikkim et Bhutan; in pratis alpinis, 10–13,000 p. s. m.

Representative in the Eastern Himalaya of the Tibetan *M. horridula*. Differs from *M. rudis* and *M. horridula* in the lobed leaves and narrow torus, from *M. aculeata* in the long capsule. Not yet known in cultivation. Probably monocarpic.

6. **Meconopsis rudis,** Prain. Folia sparse aculeata oblongo-lanceolata margine subintegra; flores in cymas racemiformes dispositi, pedicellis inferioribus bracteatis summis ebracteis; petala 5–8; capsula ovata stylo duplo longior; torus distincte ampliatus. *M. racemosa*, Franch., Bull. Soc. Bot. Fr., xxxiii. 390 (1886); Pl. Delavay., 41 (1889) nec Maxim. *M. horridula*, var. *rudis*, Prain, Journ. As. Soc. Beng., lxiv. 2. 314 (1895). *M. sinuata*, var. *Prattii*, Prain, Journ. As. Soc. Beng., lxiv. 2. 314 (1895).

CHINA AUSTRO-OCCIDENTALIS. In Yunnan et Szechuen, in pratis alpinis, 13–15,000 p. s. m.

Aculeata, spinis patentibus pallide stramineis sparse obsita. *Rhizoma* fusiforme. *Folia* radicalia pauca cito marcescentia caulina oblongo-lanceolata subacuta vel obtusa sensim in petiolum distinctum attenuata, laminis 8–10 cm. longis, 2–3 cm. latis, margine subintegris vel serratis utrinque viridibus sed subtus pallidiore, utrinque aculeatis, petiolis basi subvaginatis imis 3–5 cm. longis, summis obsoletis. *Caulis* ad 40 cm. usque altus, simplex, triente summo excepto foliosus, prope basin ·5–1 cm. crassus cylindricus, triente imo excepto laxe floriferus, prorsus sparse aculeatus. *Flores* cymosi, pedicellis aculeatis 2–5 cm. longis. *Sepala* oblongo-ovata extus densius aculeata. *Petala* 5–8, obovata oblongave, 3 cm. longa, 1–2 cm. lata, pallide coerulea, glabra. *Stamina* ∞, pluriseriata, filamentis gracillimis discretis glabris. *Ovarium* e carpellis 4 compositum, densius aculeatum; stylus pyramidalis glaber 4 mm. longus; stigma oblongum 4-sulcatum; placentae intrusae; ovula plurima. *Capsula* ovata 6 mm. longa, 5 mm. lata, aculeata in toro explanato incrassato 5 mm. lato insidens.—Yunnan; Likiang, 13,000 p. s. m., *Delavay*! Szechuen; Tachienlu, 13–15,000 p. s. m., *Pratt*, 525! *Soulie*, 635! *Wilson*, 3162!

Representative in Yunnan and Szechuen of the Tibetan *M. horridula*. Differs from *M. aculeata* and *M. sinuata* in the subentire leaves and the enlarged torus; from *M. horridula* in having a smaller capsule and having the pedicels in the lower two-thirds of the racemose cyme bracteate. Not yet known in cultivation. Probably monocarpic.

7. **Meconopsis horridula**, Hook. f. & Thoms. Folia densius aculeata lanceolata margine integra; flores in scapis rigidis dense aculeatis radicalibus discretis vel interdum basi coalitis singuli; petala saepius 5–8, nonnunquam 4; capsula ovata stylo duplo longior; torus late explanatus. Hook. f. & Thoms., Fl. Ind., 252 (1855); Walp., Ann., iv. 171 (1857); Hook. f. & Thoms., Fl. Brit. Ind., i. 118 (1872); Hemsl., Journ. Linn. Soc., xxx. 108, 134 (1894); Prain, Journ. As. Soc. Beng., lxiv. 2. 313 (1895); Hemsl., Journ. Linn. Soc., xxxv. 164 (1902); Flora and Sylva, iii. 83 (1905).

TIBET AUSTRALIS. In saxosis, supra 14,000 p. s. m. HIMALAYA ORIENTALIS. In Sikkim et Chumbi; in saxosis alpinis, supra 14,000 p. s. m.

Apparently a reduced state of the form next to be described. Not so far met with in European gardens. Apparently monocarpic.

Var. **racemosa**, Prain. Folia aculeata lanceolata margine integra vel subintegra; flores in cymas racemiformes dispositi pedicellis omnibus ebracteis vel raro pedicello imo tantum bracteato; petala 5-8; capsula ovata stylo duplo longior; torus distincte explanatus. Prain, Journ. As. Soc. Beng., lxiv. 2. 313 (1895). *M. racemosa*, Maxim., Bull. Acad. Petersb., xxiii. 310 (1876); Mel. Biol., ix. 713 (1876); Forbes & Hemsl., Journ.

Linn. Soc., xxiii. 34 (1886); Maxim., Fl. Tangut., i. 36, t. 9, figs. 1–6, t. 23, fig. 26 (1889); Flora and Sylva, iii. 84 (1905).

TIBET. In locis saxosis late dispersa. HIMALAYA ORIENTALIS. In saxosis alpinis supra 14,000 p. s. m. in Sikkim et in Chumbi cum praecedenti rara. CHINA. In saxosis alpinis supra 14,000 p. s. m. in Szechuen; in pratis alpinis in Kansuh.

Now established in European horticulture. Apparently monocarpic.

The *Aculeatae* as a whole form a natural group, most nearly related to the *Primulinae*. They differ from the latter group chiefly in being armed with rigid spines which replace the simple, rarely rigid and never pungent setae that are more or less characteristic of the *Primulinae*. They further differ in having, with the exception of *M. horridula* proper, well developed stems, whereas in the *Primulinae*, with the exception of *M. lancifolia*, we usually have simple 1-flowered scapes. At least a year appears to elapse between seed and flower in all the species of this group; the crown of leaves dies down during the intervening winter. As a rule the plant dies after flowering, but in the case of *M. aculeata* individual plants are occasionally polycarpic.

The question how far the forms that compose the *Aculeatae* are distinct species is an open one. Hooker and Thomson (Fl. Ind., 252) have suggested that the two forms which are most distinct in habit and appearance, *M. aculeata* and *M. horridula* proper, may be only varieties of one species. On the other hand, the two that are most nearly allied, *M. horridula* proper and *M. horridula* var. *racemosa*, have been treated by Maximowicz as distinct species (Mel. Biol., ix. 713 and Fl. Tangut., i. 36). The more convenient and perhaps more natural treatment adopted here lies between these two extreme views.

If further reduction be necessary it may be suggested that there are only two somewhat variable species in the group; (1) *M. aculeata*, with *M. sinuata* as a distinct variety differing in the degree of lobulation of the leaves and in the shape of the capsule; and (2) *M. horridula*, including as distinct varieties *M. racemosa* and *M. rudis*. The characters separating the two widened species are the 5–8 petals, enlarged torus, and subentire leaves in *M. horridula*, the 4 petals, unexpanded torus, and more or less lobed leaves in *M. aculeata*.

¶ 4. *Primulinae*, Prain, Journ. As. Soc. Beng., lxiv. 2. 319 (1895). Inermes; monocarpicae; caules saepissime brevissimi; folia integra; flores intense coerulei petalis saepissime 5–8, raro 4; styli distincti; stigmata saepissime globoso-clavata, raro bifida; capsula glabra vel plus minusve setosa sensim in stylum attenuata.

8. **Meconopsis lancifolia**, Franch. Folia caulibusque plus minusve setosa, lanceolata margine integra; flores in cymas racemiformes dispositi, pedicellis ebracteis; petala 4; capsula anguste obconica stylo 4-plo longior. Franch. ex Prain, Journ. As. Soc. Beng., lxiv. 2. 311 (1895). *Cathcartia lancifolia*, Franch., Bull. Soc. Bot. Fr., xxxiii. 391 (1886); Pl. Delavay., 43 (1889).

CHINA OCCIDENTALIS. Yunnan; in pratis saxosisque alpinis, 11–13,500 p. s. m.

Related to the next species, *M. Henrici*, very much as *M. racemosa* is related to *M. horridula*; perhaps, therefore, *M. Henrici* may ultimately have to be merged in this species. The specimens as yet reported appear, however, to have only 4 petals; those of *M. Henrici* almost all have more than 4; it is therefore, for the present, convenient to keep the two apart. Not yet introduced to European gardens. Apparently monocarpic.

9. **Meconopsis Henrici**, Bur. & Franch. Folia caulibusque saepius parce nonnunquam tamen dense setosa, raro glabra, lanceolata margine integra; flores in scapis pseudoradicalibus singuli vel interdum gemini; petala 6–8; capsula anguste obconica stylo 4-plo longior. Bur. & Franch., Journ. de Bot., v. 19 (1891). *M. principis*, Flora and Sylva, iii. 84 (1905).

CHINA OCCIDENTALIS. Szechuen; in pratis saxosisque alpinis, 12–14,000 p. s. m.

Sometimes quite glabrous, at other times sparingly strigose, and then very like *M. primulina*, or more or less beset with simple setae and then like *M. lancifolia*; occasionally densely clothed with rigid setae and rather like *M. horridula*: the setae, however, are not pungent. The occurrence of a second flower below the terminal flower of a scape is not infrequent; this circumstance strengthens the suspicion that *M. lancifolia* may be no more than an unusual state of a species of which *M. Henrici* is the usual form. The synonym *M. principis* used for the species in 1905 (Flora and Sylva, iii. 84) is the manuscript name originally employed by the late Mr. Franchet for the specimens subsequently described as *M. Henrici*. This has recently been introduced into European gardens, and promises to be a pleasing addition to horticulture. Apparently monocarpic.

10. **Meconopsis primulina**, Prain. Folia caulibusque parce strigosa lanceolata margine integra; flores in scapis pseudoradicalibus singuli; petala 6–8; capsula (matura ignota) anguste oblonga, glabra, vertice prope basin styli papillis obtusis induta; stigma 2-lobum. Prain, Journ. As. Soc. Beng., lxiv. 2. 319 (1895); Ann. Roy. Bot. Gard. Calcutta, ix. 1. 3, t. 3 (1901).

HIMALAYA ORIENTALIS. Chumbi et Bhutan; in pratis saxosisque alpinis, 12–14,000 p. s. m.

Very nearly allied to *M. Henrici*, and differs from that species only in having a distinctly 2-lobed stigma and in possessing two pairs of epaulette-like papillae suggestive of a rudimentary partial disk. Possibly the communication of larger suites of specimens may render it necessary to unite this plant to *M. Henrici* and to reduce both to *M. lancifolia*. In any case these three forms must be considered representative forms in three adjacent geographical areas. This form has not yet been introduced to European gardens. Apparently monocarpic.

11. **Meconopsis Delavayi**, Franch. Folia caulibusque glabra, sub-

rhomboidea obtusa margine integra vel subtiliter repanda ; flores in scapis pseudoradicalibus singuli ; petala 5–8, interdum 4 ; capsula (matura ignota) oblonga ; stylus brevis. Franch. ex Prain, Journ. As. Soc. Beng., lxiv. 2. 311 (1895). *Cathcartia Delavayi*, Franch., Bull. Soc. Bot. Fr., xxxiii. 390 (1886) ; Pl. Delavay., 42 (1889).

CHINA OCCIDENTALIS. Yunnan ; in pratis alpinis, 12,500 p. s. m.

This species is also nearly related to the preceding three forms, but differs from all of them in regard to its foliage. Not yet introduced to European gardens. Apparently monocarpic. Though very nearly glabrous, a few simple hairs are to be found on the scapes and on the leaves.

The *Primulinae* form quite as natural a group as the *Aculeatae*, to which they are most nearly allied, and with which they have already been contrasted. Here, again, it is an open question whether the forms that compose the group are really distinct species. It has been shown that there is room for suspecting that *M. Henrici* and *M. lancifolia* may only be different states of one species ; it may equally well transpire that *M. primulina* is merely an abnormal form of the same. If this can be proved the *Primulinae* will contain but two species, (1) *M. lancifolia*, including *M. Henrici* and *M. primulina*, with lanceolate leaves, and (2) *M. Delavayi*, with subrhomboid leaves. Apparently the species of this group flower in the year following sowing, the leaves dying down during the intervening winter. So far as is known they are monocarpic and die after flowering.

¶ 5. *Bellae*, Prain, Journ. As. Soc. Beng., lxiv. 2. 321 (1895). Inermes ; perennantes ; caules 0 ; folia pinnatisecta ; flores coerulei petalis 4–5 ; styli distincti ; capsula vertice circa basin styli subito quasi in discum angustum convexum astigmaticum explanata.

12. **Meconopsis bella**, Prain. Folia scapisque glabra vel minopore setosa, 2–3-secta lobulis parvis ; flores in scapis radicalibus singuli ; petala 4, raro 5 ; capsula ovata vertice ultra valvarum apices circa basin styli solida ; stylus brevis. Prain, Journ. As. Soc. Beng., lxiii. 2. 82 (1894) ; Journ. As. Soc. Beng., lxiv. 2. 321 (1895) ; Ann. Roy. Bot. Gard. Calcutta, ix. 1. 3, t. 4 (1901) ; Flora and Sylva, iii. 82. 166 (1905) ; Gard. Chron., ser. III, xl. 198, fig. 81 (1906).

HIMALAYA ORIENTALIS. Sikkim occidentalis, a finibus Nepaliae orientalibus prope, in rupibus alpinis, 12–14,000 p. s. m.

A very distinct species ; polycarpic ; the leaves persist during the winter months. There is no disk, but the tips of the valves do not quite extend to the base of the style, so that the top of the capsule is intermediate in appearance between that of a typical *Meconopsis* and that of a species of the Californian group *Anomalae*. Unlike the other species of the genus, which affect open alpine hillsides or occur among alpine scrub or on the edges of woods, *M. bella* appears restricted to more or less vertical cliffs into whose clefts the stout rootstocks grow horizontally.

This species has for some years been in cultivation at Edinburgh and perhaps elsewhere. It has flowered at Edinburgh this year (1906) for the first time.

The *Bellae* as a group must be considered quite natural. Like the *Primulinae*, and still more like the *Grandes* in habit, this group differs from both in foliage. Sometimes more than two seasons elapse between seed and flower, and in this respect the group differs from the two groups mentioned.

§ II. POLYCHAETIA. Herbae inermes pilis vel setis barbellatis indumento stellato interdum interiecto plus minusve indutae; capsula sensim in stylum attenuata vel stigmate sessili coronata, raro vertice circa basin styli in discum astigmaticum explanata; stigma clavatum lobis decurrentibus contiguis vel depresso-dilatatum lobis radiantibus divaricatis.—Herbae saepius monocarpicae; paucae tamen perennantes. *Meconopsis* § *Stylophorum*, DC. Prodr., i. 121 (1824) partim. *Polychaetia*, Wall. MSS. (gen.) ex Prain, in Journ. As. Soc. Beng., lxiv. 2. 316 (1895).

¶ 6. *Grandes*, Prain, Journ. As. Soc. Beng., lxiv. 2. 320 (1895). Caules 0 vel raro simplices scapiformes; folia integra vel subintegra plerumque vel omnia radicalia; flores pauci in scapis simplicibus aphyllis singuli vel ad apicem scapi fasciculatim foliosi in cymas umbelliformes, 3–7-floras dispositi, petalis 6–9, rarissime 4; styli saepius distincti, nonnunquam obsoleti; stigmata depresso-dilatata lobis radiantibus divaricatis; capsula plus minusve appresse setosa in stylum sensim attenuata vel subito in stigmatis plicaturas extensa.—Herbae plerumque monocarpicae, singula tamen plane perennans.

18. Meconopsis integrifolia, Franch. Caulis scapiformis versus apicem fasciculatim foliosus, raro obsoletus; folia integra; flores in cymas umbelliformes 3–7-floras dispositi, raro in scapo simplice 1-floro flos singulus medianus; petala 5–8 lutea; stylus 0; stigma latissimum (Pl. XXIV, Figs. 7, 8). Franch., Bull. Soc. Bot. Fr., xxxiii. 389 (1886); Pl. Delavay., 41 (1889); Maxim., Fl. Tangut., 35, t. 9, figs. 7–12, t. 23, figs. 22–25 (1889); Hemsl., Journ. Linn. Soc., xxxv. 164 (1902); Gard. Chron., ser. III, xxxvi. 240 c. ic. (1904); Le Jardin, xviii. 328 (1904); Bot. Mag., t. 8027 (1905); Flora and Sylva, iii. 191 c. ic. (1905). *Cathcartia integrifolia*, Maxim., Bull. Acad. Petersb., xxiii. 310 (1876); Mel. Biol., ix. 713 (1876); Forbes & Hemsl., Journ. Linn. Soc., xxiii. 34 (1886).

CHINA OCCIDENTALIS. In Kansuh, Szechuen, et Yunnan; in pratis alpinis, 13–15000 p. s. m. TIBET CENTRALIS. In valle Gooring, 16,500 p. s. m.

Hemsley has suggested that the Tibetan specimen from the Gooring Valley, originally identified by him as *M. integrifolia*, may not really belong to this species. Lipsky and the writer have, however, felt satisfied after further examination of the material that Hemsley's original determination is accurate, though the note that the flowers are 'blue' is a *lapsus calami*, for the petals in the specimen referred to are yellow. As Hemsley and Bulley have independently pointed out, the plant figured as *M. integrifolia* by Bulley in Flora and Sylva, iii. 83, is not

this species. This handsome form is now thoroughly established in European alpine gardens, where it always is monocarpic.

14. **Meconopsis pseudointegrifolia,** Prain. Caulis 0; folia integra; flores in scapis simplicibus 1-floris singuli; petala 5–8, lutea; stylus distinctus sursum incrassatus; stigma latum (Pl. XXV). *M. integrifolia,* Bulley in Flora and Sylva, iii. 80 c. ic. (1905) nec Franch.

TIBET AUSTRALI-OCCIDENTALIS. Kham; in pratis alpinis, 11–12,000 p. s. m.

Hirsuta pilis barbellatis plus minusve patentibus induta. *Folia* radicalia caespitosa 12–20 cm. longa, lanceolata vel ovato-lanceolata apice acuta margine integra, lamina 1–2·5 cm. lata in petiolum brevem basi plus minusve vaginatum sensim attenuata, utrinque viridia, laxe hirsuta. *Caulis* 0. *Flores* maiusculi pedunculis 1-floris simplicibus 12–20 cm. longis laxe hirsutis. *Sepala* 2, oblonga, extus hirsuta, 3·5 cm. longa, 2 cm. lata. *Petala* saepissime 8, lutea, ovato-oblonga, 4·5–9 cm. longa, 2–8 cm. lata, utrinque glabra. *Stamina* ∞, 3–4-seriata, filamentis glabris gracilibus discretis. *Ovarium* e carpellis 4 compositum, dense hirsutum; stylus terminalis glaber ·8–1 cm. longus, sursum plus minusve incrassatus stigmate 4-lobo terminali lobis radiantibus divaricatis coronatus; placentae parum intrusae; ovula plurima. *Capsula* matura adhuc ignota.—Kham; in valle fl. Ra-chu, a fontibus fl. Mekong prope, in lat. 29° 30′ bor., lon. 97° 30′ orient.

The description given is that of a plant presented to Kew by Mr. A. K. Bulley; this plant flowered in the Rock Garden at Kew in May, 1906. The drawing (Pl. XXV) was made by Miss M. Smith from this plant. Another example of the same species flowered at Neston in 1905 and was figured in 'Flora and Sylva.' These plants were raised from seed received by Bulley from the Imperial Botanic Garden, St. Petersburg. The seeds were sent to St. Petersburg by Captain Koslov from south-eastern Tibet, from the valley of one of the headwaters of the Mekong.

In colour of petals, and in shape and degree of tomentum of leaves, this much resembles *M. integrifolia.* It differs, however, from *M. integrifolia* in all the scapes being simple, radical, and 1-flowered, and in having a distinct style with a narrower stigma. The difference in habit between *M. pseudointegrifolia* and *M. integrifolia* is paralleled in the case of *M. simplicifolia* and *M. grandis.*

This species has not ripened seeds, at all events in England. Apparently monocarpic.

15. **Meconopsis grandis,** Prain. Caulis e rhizomate perennante scapiformis versus apicem fasciculatim foliosus; folia grosse paucidentata; flores in cymas umbelliformes 3-floras dispositi, nonnunquam floribus 1–2 axillaribus in parte caulis inferiore adiectis; petala 6–9 fusco-purpurea vel nonnunquam intense coerulea; stylus distinctus; stigma latum. Prain, Journ. As. Soc. Beng., lxiv. 2. 320 (1895); Ann. Roy. Bot. Gard. Calcutta, ix. 1. 2, t. 2 (1901); Gard. Chron., ser. III, xxxvii. 369, fig. 157 (1905); Flora and Sylva, iii. 82 (1905).

HIMALAYA ORIENTALIS. Sikkim occidentalis; in pratis alpinis a finibus Nepaliae orientalibus prope, 10–12,000 p. s. m.

This species is like *M. integrifolia* in having a scape-like stem with a cluster of sessile leafy bracts at the apex and generally two flowers there in addition to the terminal one. On the scape below the apical cluster there are usually a few scattered sessile leaves, occasionally in the axils of the highest of these are other flowers. *M. grandis*, however, differs from *M. integrifolia* in having a distinct style, purple not yellow flowers, coarsely toothed not entire leaves, and a sparsely not densely setose capsule.

M. grandis is now quite established in a few European alpine gardens, more particularly at Edinburgh, where one old plant had, up to 1906, flowered in at least twelve successive seasons. Usually polycarpic.

16. **Meconopsis simplicifolia,** Walp. Caulis 0; folia integra vel remote dentata; flores in scapis simplicibus 1–floris singuli; petala 6–8, coerulea; stylus distinctus; stigma latum. Walp., Rep., i. 110 (1842); Hook. f. & Thoms., Fl. Ind. 252 (1855); Hook. f., Ill. Him. Pl., t. 8 (1855); Ill. Hortic., iii. 114 (1856); Walp., Ann., iv. 170 (1857); Fl. des Serres, xiii. t. 1324 (1858); Hook. f. & Thoms., Fl. Brit. Ind., i. 118 (1872); Prain, Journ. As. Soc. Beng., lxiv. 2. 321 (1895); Flora and Sylva, iii. 84 (1905). *Papaver simplicifolium*, D. Don, Prodr. Fl. Nepal., 196 (1825). *Stylophorum simplicifolium*, Spreng., Syst., iv., cur. post. 203 (1827); G. Don, Gen. Syst., i. 135 (1831); Steud., Nomencl., ed. 2, ii. 650 (1841).

HIMALAYA CENTRALIS ORIENTALISQUE. Nepal, Sikkim, Chumbi, Bhutan; in pratis alpinis, 12–16,000 p. s. m. TIBET AUSTRALIS. Khamba et Phari; in pratis alpinis 14–15,000 p. s. m.

In habit and general appearance *M. simplicifolia* agrees with *M. pseudointegrifolia*, as regards fruit it agrees with *M. grandis*. To the latter species it bears somewhat the relationship that the former bears to *M. integrifolia*. The species has long been well known in European alpine gardens. Apparently always monocarpic.

17. **Meconopsis quintuplinervia,** Regel. Caulis 0; folia integra; flores in scapis simplicibus 1–floris singuli, nutantes; petala 4, purpurea; stylus distinctus; stigma latum. Regel, Gartenfl., xxv. 291, t. 880, figs. b, c, d (1876); Maxim., Fl. Tangut., 34, t. 23, fig. 27 (1889); Flora and Sylva, iii. 84 (1905).

CHINA OCCIDENTALIS. Kansuh; in pratis alpinis, 9,500–11,000 p. s. m. TIBET BOREALI-ORIENTALIS. Amdo; in pratis alpinis, 9,500–11,000 p. s. m.

This species is nearly allied to *M. simplicifolia* but differs somewhat in foliage, and more considerably in number and colour of petals, also in number of stamens which are here fewer and subbiseriate instead of several-seriate. The capsule

in this species is more closely covered with setae. By an oversight, the locality for this plant is given in the 'Index Kewensis' as Mandshuria; this error has been copied in 'Flora and Sylva.' No species of *Meconopsis* occurs in Mandshuria, and its true locality, Kansuh, is correctly given by Regel with the original description of this one.

This species was introduced to European gardens in 1876 but, like *M. pseudo-integrifolia*, died down without ripening seeds. Apparently monocarpic.

18. **Meconopsis punicea**, Maxim. Caulis 0; folia integra; flores in scapis simplicibus 1–floris singuli, penduli; petala 4, rarissimo in speciminibus cultis 8–9, punicea; stylus 0; stigma latissimum. Maxim., Fl. Tangut., 34, t. 23, figs. 12–21 (1889); Gard. Chron., ser. III, xxxvi. 289, fig. 130 (1904); Flora and Sylva, iii. 84 (1905).

CHINA OCCIDENTALIS. Szechuen; in pratis alpinis, 12,000 p. s. m. TIBET BOREALI-ORIENTALIS. In valle Djao-chu.

This species, like *M. integrifolia*, has a large sessile divaricately-lobed stigma, with no disk. It differs in having simple 1-flowered scapes with very dark pink flowers, which are pendulous even when fully opened. Usually there are only 4 petals; the example figured in the 'Gardeners' Chronicle' had, however, 8 to 9. This species is now fairly well established in alpine collections. Apparently monocarpic.

The *Grandes* constitute a natural group different from the other groups of the section *Polychaetia*, but in habit resembling the *Bellae* and the *Primulinae* in the section *Eumeconopsis*. From all other groups, except a single species in the group *Chelidonifoliae*, they stand apart as regards the character of the stigma, the lobes of which are divaricately radiant instead of contiguously decurrent. *M. grandis* is unlike the other species of the group, and is somewhat exceptional in the genus as a whole, in being usually polycarpic; all the others in cultivation have proved monocarpic. All the species appear to flower, as a rule, one year from seed, the leaves dying down during the intervening winter. As a rule also, plants of the monocarpic species that do not flower at the proper time die along with those that do flower; under exceptional circumstances they may survive till another season and flower then.

¶ 7. *Torquatae*, Prain. Caules elongati simplices scapiformes; folia subintegra plerumque radicalia; flores numerosi in cymas compactas subspiciformes dispositi; styli distincti vel brevissimi; stigmata oblonga vel clavata lobis decurrentibus contiguis; capsula appresse setosa vertice circa basin styli disco glabro lobato coronata.

19. **Meconopsis torquata**, Prain. Folia plerumque radicalia margine integra vel subintegra; flores brevissime pedicellati vel sessiles; petala extus parce hirsuta; ovarii discus sinuatus et obtuse angulatus lobis integris; stylus perbrevis stigmate ovato brevior (Pl. XXIV, Fig. 11).

TIBET AUSTRALIS. In pratis alpinis, 11,500 p. s. m.

Hirsuta pilis patentibus aureo-fuscis basi glanduloso excepto barbellatis induta. *Rhizoma* an perennans? vaginis numerosis foliorum anni praecedentis obsitum.

Folia plurima caespitosa radicalia et subbasalia pauca tamen sparse caulina, ea trientis caulis imi basalibus conformia sed minora, trientis medii parva bracteiformia sed 5–6 summis floriferis exceptis vacua; radicalia et subbasalia 10–12 cm. longa, spathulata obtusa vel subacuta, margine integra vel remote irregulariterque subsinuata, lamina 1·25–1·75 cm. lata in petiolum 3–4 cm. longum basi plus minusve vaginatum attenuata, supra pallide viridia subtus glaucescentia utrinque sed praesertim subtus petioloque hirsuta; caulina inferiora 4–6 cm. longa, lamina ·75 cm. lata, petiolo ·75–1·5 cm. longo, superiora bracteiformia irregulariter lobata 1·5 cm. long, ·5 cm. lata, sessilia. *Caulis* ad 40 cm. usque altus, simplex, scapiformis, basi minimo digito crasso cylindricus, sursum praesertim triente summo dense florifero plus minusve sulcatus, prorsus hirsutus. *Flores* numerosi versus apicem caulis subspicatim aggregati, inferiores tantum bracteati; pedicellis obliquis hirsutis ·5 cm. longis vel brevioribus nonnunquam obsoletis. *Sepala* nondum obvia. *Petala* 4 (an semper?), pallide punicea, oblongo-ovata ad 4 cm. usque longa, 2·5 cm. lata, extus sparse hirsuta intus glabra. *Stamina* ∞, 2–3-seriata, filamentis glabris gracilibus discretis. *Ovarium* e carpellis 8 compositum, dense setosum ovoideum disco glabro puniceo-purpurascente margine 8-sinuato et obtuse 8-angulato subplicatim explanato et plane astigmatico coronatum; stylus centralis perbrevis; stigma ovatum integrum lobis contiguis; placentae valde intrusae; ovula plurima. *Capsula* ovoidea plus minusve angulata, 1·35 cm. longa, 1 cm. lata, sub margine disci poris 8 dehiscens. *Semina* plurima, vix matura, ovoidea 2 mm. longa, ·75 mm. lata, testa reticulata.—Tibet: In valle fl. Kyi-chu, 11,500 p.s.m., a Lhasa prope; in mense Septembri florens, *Walton*!

Closely allied to the next species, from which it differs only in the shorter pedicels, the much shorter style, the ovate instead of rather narrowly clavate stigma, and the entire in place of toothed disk-margin.

20. **Meconopsis discigera**, Prain. Folia radicalia margine versus apicem parce grosseque dentata; flores distincte pedicellati, pedicellis capsulam aequantibus; ovarii discus sinuatus et acute angulatus lobis denticulatis; stylus distinctus stigma clavatum aequans (Pl. XXIV, Fig. 12).

HIMALAYA ORIENTALIS. Sikkim occidentalis; in pratis alpinis, 11-12,000 p. s. m.

Hirsuta pilis patentibus aureo-fuscis barbellatis induta. *Rhizoma* an perennans? vaginis foliorum anni praecedentis obsitum. *Folia* perplurima caespitosa radicalia, 10–15 cm. longa, spathulata subacuta, margine versus apicem pauce grosse dentata vel sublobata, lamina 1·75–2 cm. lata in petiolum 6–8 cm. longum basi plus minusve vaginatum attenuata, supra viridia subtus glaucescentia utrinque petioloque hirsuta; bracteae foliaceae lanceolatae ad 4·5 cm. usque longae, ·5 cm. latae. *Caulis* ad 30 cm. usque altus, simplex, scapiformis, basi ·5 cm. crassus cylindricus sursum praesertim dimidio superiore densius florifero plus minusve sulcatus, prorsus hirsutus. *Flores* racemosi; pedicellis hirsutis 2 cm. longis. *Sepala* ignota. *Petala* ignota. *Stamina* ∞, pluri-seriata, filamentis glabris gracilibus discretis. *Ovarium* e carpellis 6–8 compositum, dense hirsutum, disco glabro margine acute angulato, denticulato,

explanato, plane astigmatico coronatum; stylus centralis glaber ·5 cm. longus; stigma clavatum, plus minusve 2-lobum, ·6 cm. longum; placentae intrusae; ovula plurima. *Capsula* oblonga 6–8-angula 1·75–2 cm. longa, ·8 cm. lata sub disci margine poris 6–8 dehiscens. *Semina* plurima, ovoidea, 2 mm. longa, ·75 mm. lata, testa reticulata.—Sikkim: Gucha-la, 11–12,000 p. s. m., in mense Septembri fructifera, *Cave*!

Nearly allied to the preceding species, from which it differs in the points already noted. Seedlings of this species have been raised at Kew and at Edinburgh; its establishment in European gardens is therefore to be hoped for.

The *Torquatae* form a natural and striking group. Their habit recalls that of the *Aculeatae* of the section *Eumeconopsis*, with however more numerous and more closely set flowers, so that, especially in *M. torquata*, the cymes are spicate rather than racemose. As compared with the other groups of the section *Polychaetia*, in which the hairs are of the same character (see Pl. XXV, Fig. 3), the *Torquatae* agree with the *Grandes* as regards foliage, with the *Robustae* in having numerous flowers. In the *Robustae*, however, the stems are tall and stately, are leafy throughout, and bear their flowers in loose racemose or paniculate, not in congested or subspicate cymes. As in the case of the group *Bellae*, the very stout rhizomes and the plentiful remains of old leaves suggest the possibility that the *Torquatae* may be perennials; there is, however, as yet no direct proof that they are other than monocarpic, and it may be that the explanation is merely that the species of this group do not flower till several years from seed have elapsed.

¶ 8. *Robustae*, Prain, Journ. As. Soc. Beng., lxiv. 2. 315 (1895). Caules magnopere evoluti elati plerumque copiose ramosi; folia grosse dentata vel varie lobata caulina numerosa sparsa; flores numerosi in cymas laxas racemiformes paniculatasve dispositi, petalis 4; styli distincti; stigmata clavata lobis decurrentibus contiguis; capsula nunc appresse nunc patenter setosa in stylum sensim attenuata.—Herbae monocarpicae.

21. **Meconopsis superba**, King. Folia radicalia sinuato-lobata caulina grosse dentata laxe pilis barbellatis simulac dense indumento stellato induta; sepala laxe strigosa et dense stellato-tomentosa; flores albi in cymas racemiformes dispositi; capsula valvis 8–11 appresse setosa et dense stellato-tomentosa; stylus brevis basi manifeste incrassatus. King ex Prain in Journ. As. Soc. Beng., lxiv. 2. 317 (1895); Ann. Roy. Bot. Gard. Calcutta, ix. 1. 4, t. 5 (1901). *M. nepalensis*, Flora and Sylva, iii. 84 (1905) partim et quoad exempla albiflora prolata.

HIMALAYA ORIENTALIS. Bhutan; in pratis alpinis, 10–11,000 p. s. m.

Very nearly related to *M. paniculata* and apparently only a representative of that species in a locality somewhat further to the east. The habit and foliage are exactly as in *M. paniculata*, but the stems appear to be taller and stouter even than in that species, and the flowers, which are larger, are white. Whether this has been introduced to European gardens is not clear; it is reported (Flora and Sylva, iii. 84) that a *Meconopsis* bearing large bell-shaped flowers of an ivory-white

has been met with in cultivation. The plant is treated, in the passage referred to, as a form of *M. nepalensis* (i. e. of the plant here termed *M. paniculata*, not of the true red-flowered *M. napaulensis*), but no reference is given to the collection in which this white-flowered plant has existed, and no definite authority for the statement is quoted. In all probability *M. superba*, like the other members of the group *Robustae*, is monocarpic.

22. **Meconopsis paniculata**, Prain. Folia radicalia sinuato-lobata raro pinnatifida, caulina grosse dentata vel interdum parum lobata laxe pilis barbellatis simulac dense indumento stellato induta; sepala laxe strigosa et dense stellato-tomentosa; flores lutei, in cymas racemiformes dispositi; capsula valvis 8–11 appresse setosa et dense stellato-tomentosa; stylus brevis basi manifeste incrassatus. Prain, Journ. As. Soc. Beng., lxiv. 2. 316 (1895). *M. napaulensis*, Walp., Rep., i. 110 (1842) non DC. *M. Wallichii*, Hook. f. & Thoms., Fl. Ind., 254 in parte (1855); Walp., Ann., iv. 171 in parte (1857); Hook. f. & Thoms., Fl. Brit. Ind., i. 119 in parte (1872)—quoad exemplum sub Wall. Cat., 8123/b prolatum, non Hook. *Papaver paniculatum*, D. Don, Prodr. Fl. Nepal., 197 (1825)—quoad descriptionem sed syn. *Meconopsis napaulensis* excl. *Stylophorum paniculatum*, G. Don, Gen. Syst., i. 135 in parte (1831) et quoad exempla floribus luteis prolata tantum. *S. nepalense*, Steud., Nomencl., ed. 2, 650 in parte (1841). *Polychaeta paniculata*, Wall. ex Prain, Journ. As. Soc. Beng., lxiv. 2. 316 (1895).

HIMALAYA CENTRALIS ORIENTALISQUE. Nepal, Sikkim, et Bhutan; in pratis alpinis, 10–11,000 p. s. m.

Hardly separable even as a variety from the next form, owing to the existence of numerous intermediates.

Var. **elata**, Prain. Flores in cymas laxe paniculatas dispositi, caeterum typi. Prain, Journ. As. Soc. Beng., lxiv. 2. 316 (1895). *M. nipalensis*, Hook. f. & Thoms., Fl. Ind., 253 (1855); Hook. f., Ill. Him. Pl., t. 9 (1855); Walp., Ann., iv. 171 (1857); Hook. f. & Thoms., Fl. Brit. Ind., i. 118 (1872) nec *M. napaulensis*, DC. *M. nepalensis*, Lem., Ill. Hortic., iii. 95 (1856); Flora and Sylva, iii. 83 (1905), nec *M. napaulensis*, DC. *M. Wallastonii*, Regel, Gartenfl., xxv. 291 (1876) nomen tantum.

HIMALAYA CENTRALIS ORIENTALISQUE. Nepal et Sikkim; in pratis alpinis, 10–11,000 p. s. m.

This form is treated here as a variety, rather as a matter of convenience than of necessity. The two are easily distinguished in their extreme states; they, however, pass insensibly into each other. By keeping them apart it is more easy to disentangle the confused synonymy that has resulted from the erroneous reduction by Don, to one of them, of De Candolle's very different *M. napaulensis*.

The species is familiar in European alpine gardens. Apparently always monocarpic.

23. **Meconopsis robusta,** Hook. f. & Thoms. Folia radicalia pinnatipartita caulina pinnatifida glaucescentia pilis barbellatis sparse strigosa; sepala laxe strigosa; flores lutei in cymas racemiformes paniculatasve dispositi; capsula valvis 8–11 laxe patenter setosa; stylus brevis basi manifeste incrassatus. Hook. f. & Thoms., Fl. Ind., 253 (1855); Walp., Ann., iv. 171 (1857); Prain, Journ. As. Soc. Beng., lxiv. 2. 315 (1857); Strachey, Pl. Kumaon, 10 (1906). *M. nipalensis*, Hook. f., Bot. Mag., t. 5585 (1866), nec *M. napaulensis*, DC. *M. robusta*, Hook. f. & Thoms., Fl. Brit. Ind., i. 118 (1872), pro parte maxima sed exemplum nepalense prolatum excludend. *M. paniculata*, Flora and Sylva, iii. 84 (1905) nec Prain. *Argemone mexicana*, Wall. in Cat. Lith., 8126 E (1830) nec Linn.

HIMALAYA OCCIDENTALIS. Garhwal et Kumaon; in pratis alpinis, 8–12,000 p. s. m.

M. robusta is nearly allied to *M. paniculata* and is the representative of that species in the western Himalaya. It is readily distinguished from *M. paniculata* and *M. superba* by its more deeply lobed leaves and by the absence of stellate pubescence; with both it agrees as regards the shape of the capsule and style. As regards foliage, though not as regards indumentum, it agrees with *M napaulensis* and *M. Wallichii*, rather than with *M. paniculata*; from these two, however, it differs markedly in respect to the shape of the capsule and style.

Occasionally to be met with in European collections, this appears to be as a rule confused with *M. paniculata*. The latest instance of this confusion (Flora and Sylva, iii. 84) corrects itself. The remark that the foliage of the plant referred to is 'much cut' shows that the author cannot have had the true *M. paniculata* in view. Besides, in the article referred to, the true *M. paniculata* is already accounted for under the erroneous name *M. nepalensis*. Apparently always monocarpic.

24. **Meconopsis napaulensis,** DC. Folia radicalia pinnatipartita caulina pinnatifida laxe pilis barbellatis simulac dense indumento stellato induta; sepala laxe strigosa et dense stellato-tomentosa; flores fusco-purpurei in cymas paniculatas dispositi; capsula valvis 5–7 patenter vel subreflexe setosa; stylus elongatus subcylindricus. DC. Prodr., i. 121 (1824); Prain, Journ. As. Soc. Beng., lxiv. 2. 317 (1895). *M. robusta*, Hook. f. & Thoms., Fl. Brit. Ind., i. 118 (1872) pro parte minima et quoad exemplum nepalense (Wall. Cat., 8121) prolatum, nec *M. robusta*, Hook. f. & Thoms. in Fl. Ind. *M. Wallichii*, var. *rubrofusca*, Hook. f., Bot. Mag., t. 6760 (1884). *Stylophorum nepalense*, Spreng., Syst., iv., cur. post. 203 (1827); Steud., Nomencl., ed. 2, ii. 650 (1841) partim. *S. paniculatum*, G. Don, Gen. Syst., i. 135 (1831), partim et quoad exempla floribus rubris prolata.

HIMALAYA CENTRALIS ORIENTALISQUE. Nepal et Sikkim occidentalis; in pratis alpinis, 10–12,000 p. s. m.

This species resembles *M. robusta* in foliage, and specimens corresponding to the original type were in 1872 referred by Hooker and Thomson to that species,

It resembles still more closely *M. Wallichii*, with which it agrees not only in shape of leaves but in shape of capsule and style, and living examples were in 1884 treated by Sir J. D. Hooker as the basis of his *M. Wallichii*, var. *rubrofusca*. It has recently been stated (Flora and Sylva, iii. 85) that a large proportion of seedlings from home-saved seed of *M. Wallichii*, which has blue flowers, often turn out as shades of dirty purple and brown. If this observation were confirmed—it is not, however, stated on what or on whose authority it is made—it would appear as if *M. Wallichii* were not even varietally separable from *M. napaulensis*. At Kew, however, the writer is informed by Mr. Irving, the occurrence reported only happens when seed is taken from plants of *M. Wallichii* which have been growing alongside of plants of *M. napaulensis*; otherwise both plants come true to seed. The two are undoubtedly representative species, but *M. napaulensis* appears to cease in western Sikkim where *M. Wallichii* begins.

M. napaulensis appears to have been known in European gardens before 1831. At all events, G. Don was aware that there were two Nepalese plants, one with yellow, the other with red flowers, so like each other in general appearance that he felt constrained to treat them as forms of a single species, *Stylophorum paniculatum*. Seeds of both may quite well have reached Europe from Nepal with the other seeds that we know from various sources to have been dispatched from that country by Wallich. When the nature of Wallich's herbarium specimens of the two plants is considered, it is not conceivable that G. Don could have learned, certainly D. Don six years previously did not know, that there were both yellow-flowered and red-flowered paniculate poppies in Nepal, unless living examples had somewhere and somehow come under his notice. There is, however, no definite record of the flowering of *M. napaulensis* in Europe till 1884, when a plant, raised from seed sent from Sikkim by Sir G. King, flowered with the late Mr. Wilson at Weybridge. Since that date *M. napaulensis* has become well established in English gardens. Apparently always monocarpic.

25. **Meconopsis Wallichii**, Hook. Folia radicalia pinnatipartita caulina pinnatifida laxe pilis barbellatis simulac dense indumento stellato induta; sepala dense stellato-tomentosa rarius etiam laxe strigosa; flores coerulei in cymas paniculatas dispositi; capsula valvis 5–7 primum appresse deinde patenter setosa; stylus elongatus subcylindricus (Pl. XXIV, Fig. 6). Hook., Bot. Mag., t. 4668 (1852); Jard. Fleur., iii. t. 315 (1853); Belg. Hortic., iv. t. 18 (1854); Fl. des Serres, viii. t. 735 (1855); Hook. f. & Thoms., Fl. Ind., 254 (1855); Walp., Ann., iv. 171 (1857); Hook. f. & Thoms., Fl. Brit. Ind., i. 119 (1872) omnes partim et quoad exemplum sikkimense floribus coeruleis prolatum sed exemplo nepalensi (Wall. Cat., 8123/b = *Polychaetia paniculata*, Wall.), cui flores lutei, excluso; Dym. Ward. & Hoop., Pharmacogr. Ind., i. 112 (1889); Prain, Journ. As. Soc. Beng., lxiv. 2. 318 (1895); Flora and Sylva, iii. 84 c. ic. (1905).

HIMALAYA ORIENTALIS. Sikkim, Chumbi et Bhutan; in pratis alpinis, 10–12,000 p. s. m. CHINA OCCIDENTALIS. Szechuen; in pratis alpinis, 12,000 p. s. m.

This species in habit and general appearance agrees almost as closely with *M. napaulensis* as does *M. Oliveriana* with *M. chelidonifolia.* In the present instance, indeed, the parallelism extends to the ovary and the fruit, which are, when quite ripe, barely distinguishable. There is a slight difference in tomentum; there are fewer long barbellate hairs on the leaves of *M. Wallichii* than on those of *M. napaulensis*, and usually, though not always, the sepals of *M. Wallichii* have only a close-felted stellate tomentum, the long barbellate hairs being absent. This, however, is neither a sufficiently distinct nor a sufficiently constant character to warrant the separation of the two, and the most definite distinction lies in the colour of the flowers, blue in *M. Wallichii*, red in *M. napaulensis*. Though it is reported that, when the two are grown side by side, seed produced by plants of *M. Wallichii* may result in plants with flowers like those of *M. napaulensis*, it is remarkable that intermediates have not been recorded. It is further to be observed that *M. Wallichii* has never been collected in central or eastern Nepal where *M. napaulensis* appears to be common, and that, on the other hand, *M. napaulensis* does not extend eastward from western Sikkim into the area in which *M. Wallichii* is a characteristic species. In horticulture the two must always be distinguished; it seems, therefore, preferable to continue to treat them as specifically separable.

This species was originally introduced to European gardens by Sir Joseph Hooker more than half a century ago. It is now perhaps the most familiar and most thoroughly established of all the Asiatic species of *Meconopsis*. Apparently always monocarpic.

The *Robustae* form a distinct and natural group; all of the species have tall leafy stems rarely less than 4–5 feet, often as much as 8–10 feet high, with numerous flowers disposed in laxly raceme-like or paniculate cymes. The flowers are 'papaveroid,' no tendency to an increased number of petals has ever been observed in the group; the capsules, styles and stigmas are typical of the genus. The group stands almost alone in the fact that as a rule they do not flower till the second year from seed, and that during the two intervening winters the rosette of leaves persists. Apparently all die after flowering.

The synonymy, as will be seen from the citations under the various species, has been much confused. This is perhaps hardly to be wondered at when the distribution within the group of its characteristic features is taken into consideration. Disregarding for the moment the colour of the petals, we find that while all are beset with barbellate hairs four of the *Robustae* have also a close-felted stellate tomentum. By this character therefore we obtain two sub-groups consisting of (1) *M. robusta* itself without this felted tomentum, and (2) *M. superba*, *M. paniculata*, *M. napaulensis* and *M. Wallichii* with it. If, however, we neglect the tomentum and consider the character of the ovary and capsule we have again two sub-groups; (1) including *M. robusta*, *M. superba*, and *M. paniculata*, with eight or more valves, with a short style thickened considerably at the base and with persistently adpressed setae; and (2) including *M. napaulensis* and *M. Wallichii* with seven or fewer valves, with a longer and more slender style, and with ultimately spreading setae. If, on the other hand, we consider the character of the foliage apart from the tomentum, we find again two sub-groups; (1) including *M. superba* and *M. paniculata*, with the leaves slightly

lobed or only toothed; (2) including *M. robusta*, *M. napaulensis*, and *M. Wallichii*, with much divided leaves. Of these three alternative groupings, that which is based on the differences as regards gynoecium and fruit is doubtless the most natural; it has the further advantage of according best with the differences as regards colour of petals, for the forms with 8–11-valved ovaries and persistently adpressed setae have the flowers yellow or ivory-white, the forms with 5–7-valved ovaries and ultimately spreading setae have the petals blue or red. If, therefore, reduction be insisted upon, we may with some justification recognize but two species, viz.:— 1, *M. paniculata*, including, as a variety, *M. superba*, and, as a subspecies, *M. robusta*; 2, *M. napaulensis*, including, as a variety, *M. Wallichii*. The confusion indicated by the synonymy has not, however, been altogether the result of a difficulty in deciding which of these mutually incompatible differential characters may be the more important. It has largely had a purely bibliographical origin and has resulted from the reduction by D. Don (Prodr. Flor. Nepal., 197) of De Candolle's *Meconopsis napaulensis* to his own *Papaver paniculatum*, which is *Meconopsis paniculata*. Why Don made this suggestion is not at all clear; his account of *M. paniculata* is by no means unsatisfactory; even if it had been so, an accident has made the misidentification of Don's species impossible. His description does not tally with De Candolle's brief diagnosis of *M. napaulensis*, and an examination of De Candolle's original specimen shows that the two are different, both as regards foliage and as regards fruit. Don's erroneous reduction has, however, been so generally followed, that in horticulture it has become usual to associate De Candolle's name for the red-flowered member of this group with sometimes one, sometimes another of the yellow-flowered ones. The writer attempted in 1895 (Journ. As. Soc. Beng., lxiv. 2. 317, 318) to unravel this somewhat tangled skein, and tried to make it clear that what has so often been taken for *M. napaulensis* is really *M. paniculata*. A reference to one of the most recent resumés of our information with regard to this genus Flora and Sylva. iii. 81–84) shows, however, that the old confusion is still perpetuated, and that the only result of the writer's previous note on the subject has been to originate a new confusion; the name 'M. nepalensis,' which belongs to a red-flowered species, is still associated with one of the yellow-flowered ones, and the name 'M. paniculata,' which belongs to this yellow-flowered one, has been transferred to a second yellow-flowered species which has already been properly named and accurately described by Hooker and Thomson as *M. robusta*. Under the circumstances it seems advisable to state the facts once more as explicitly as possible.

The specimen on which De Candolle based his diagnosis of *M. napaulensis* was collected by Wallich in Nepal in 1819, and was sent by him to Geneva prior to 1824. De Candolle's diagnosis, though brief, is, when taken in conjunction with collateral evidence, adequate for the recognition of the plant.

It has been shown under *M. aculeata* that Jacquemont believed the plant which Royle subsequently so named to be De Candolle's *M. napaulensis*, that Honigberger also held this view, and that at a later date Falconer was of the same opinion. Possibly these botanists were led to this conclusion because De Candolle has described *M. napaulensis* as being 'capsulis valde echinatis,' a phrase appropriate to the prickly capsules of *M. aculeata*. However, De Candolle's references to the style

and to the indumentum of *M. napaulensis* prove that his species cannot be Royle's *M. aculeata*. Moreover, when it is recollected that De Candolle uses the phrase 'capsulis echinatis' with regard to his *Meconopsis petiolata*, which is *Chelidonium diphyllum*, Michx., it will be realized that he does not necessarily imply that the capsules of *M. napaulensis* are prickly; and an examination of the actual specimen which De Candolle had before him shows that its capsules are not prickly and that it is not the plant named *M. aculeata* by Royle.

D. Don, a year after De Candolle's diagnosis was published, described two Nepalese species of *Meconopsis* from specimens sent by Wallich to Lambert at the same time that *M. napaulensis* was sent by Wallich to De Candolle. One of these two had been named *Polychaetia paniculata* by Wallich before the specimens left India. For some reason Wallich did not send examples of either of these two species to De Candolle; on the other hand, Wallich evidently sent no example of *M. napaulensis* to Lambert. Don did not admit that *Meconopsis* was generically distinct from *Papaver*; it is therefore not surprising that he could not follow Wallich in considering *Polychaetia* separable from *Meconopsis*. But Don did take up Wallich's manuscript specific name *paniculata*—a circumstance so far fortunate, since it enables us, knowing as we do the plant to which Wallich gave the name *Polychaetia paniculata*, to state with certainty what the plant described by Don as *Papaver paniculatum* really is.

When in 1830 Wallich distributed, independently of his communications at an earlier date to De Candolle and to Lambert, specimens of all the species of *Meconopsis* in the Calcutta Herbarium, he issued them under the following numbers:—8121, 8122, 8123/a, 8123/b, 8124, 8125, and 8126/E. The last of these numbers, collected in Kumaon, is *M. robusta*, Hook. f. and Thoms.; it is evident that its issue under the name *Argemone mexicana* was a mere accident. Of the others 8125, from Nepal, is *M. simplicifolia*, Walp., not previously sent to De Candolle, though it was previously sent to Lambert, in whose herbarium Don named and described it as *Papaver simplicifolium*; 8124, collected in Kumaon by Blinkworth, but neither sent to De Candolle nor to Lambert, is *M. robusta*, Hook. f. and Thoms. The plant from Nepal to which Wallich in India attached the name *Polychaetia paniculata*, was issued in 1830 under the Catalogue number 8123/b; this plant, though not sent to De Candolle before 1824, was previously communicated under this manuscript name to Lambert, and was consequently described by Don as *Papaver paniculatum*. As regards the locality of 8123/a Wallich seems to have been in doubt; the entry against it in the Catalogue is 'Kumaon?'. There is, however, no doubt with regard to its identity; it is not *M. robusta*, Hook. f. and Thoms., the only species of this group that, so far as we know, occurs in Kumaon; it is a form of, and is hardly varietally separable from, *M. paniculata*. The next number, 8122, from Kumaon, is *M. aculeata*, Royle, and calls for no remark. The only other number, 8121, which came from Nepal, is found on comparing it with the specimen in the Prodromus Herbarium at Geneva to be the plant which Wallich had previously sent to Geneva at the time that he sent *M. simplicifolia* and *M. paniculata* to Lambert, and is therefore the plant that De Candolle described as *M. napaulensis*.

The reduction by D. Don of this species, specimens of which he clearly had never seen, to his own very distinct *Papaver paniculatum* has already been commented

on. How little real ground there was for the reduction may be gathered from the treatment accorded to the two plants by Hooker and Thomson. These authors, it is true, have nominally accepted Don's reduction of *M. napaulensis* to *Papaver paniculatum*. But they have pointed out (Flor. Ind., 253) that De Candolle's description of *M. napaulensis* tallies better with that of their own species *M. robusta* than it does with that of Don's *Papaver paniculatum*, which is their *M. nipalensis*. In 1855, when this remark was published, Hooker and Thomson did not account for Wallich's 8121, which we know now is the true *M. napaulensis*; when, however, in 1872, the same authors (Flor. Brit. Ind., i. 118) did deal with the actual specimens of what—though they did not yet know this fact—is *M. napaulensis*, it is significant that it was to their own *M. robusta*, not to their own *M. nipalensis*, that they referred the plant. Apart, however, from the fact that the indumentum of Wallich's 8126/E and 8124, which really belong to *M. robusta*, Hook. f. and Thoms., is not the same as the indumentum of Wallich's 8121, which really belongs to *M. napaulensis* DC., and that though the foliage of the two is similarly divided the capsules and styles are different, we now know that *M. robusta* has yellow flowers like those of *M. paniculata*, and that the flowers of *M. napaulensis* are red. The position of *M. napaulensis*, as a species distinct from either of the yellow-flowered members of the group *Robustae*, is now established beyond dispute, and the question at issue is no longer whether *M. napaulensis* is, or is not, different from *M. paniculata* or *M. robusta*, but whether the blue-flowered Sikkim Poppy, *M. Wallichii*, so familiar in alpine gardens, is really specifically distinct from the much older, though less perfectly understood red-flowered *M. napaulensis*. When, in 1884, *M. napaulensis* flowered in England for the first time, as to which we have a definite record, Sir J. D. Hooker had no hesitation in treating it as a variety of *M. Wallichii*. That the two are closely allied is certain, and that they are representatives the one of the other in immediately adjacent areas is true. The form that the necessary reductions will take, if they must be effected, has been indicated. From the cultural point of view, however, these reductions would hardly be beneficial; the writer therefore prefers to leave these various forms as they are.

¶ 9. *Chelidonifoliae*, Prain, Journ. As. Soc. Beng., lxiv. 2. 313 (1895) *M. cambrica* excludenda. Inermes; perennantes; caules elongati ramosi foliosi; folia pinnatifida sparse hirsuta; flores lutei petalis 4; stylus nunc stigmate globoso-clavato distinctus, nunc stigmate depresso-dilatato subobsoletus; capsula glabra sensim in stylum attenuata vel subito in stigmatis plicaturas extensa.

26. **Meconopsis chelidonifolia**, Bur. & Franch. Rhizoma villosum; folia ovato-oblonga segmentis ovatis lobis obtusis vel subobtusis, caulibusque sparse strigosa; sepala glabra; capsula ovata stylo distincto. Bur. & Franch., Journ. de Bot., v. 19 (1891); Flora and Sylva, iii. 82 (1905).

CHINA OCCIDENTALIS. Szechuen occidentalis; in dumetis et umbrosis, 13,000 p. s. m.

In every character except the fruit this plant is quite like *M. Oliveriana*. In this species the fruit is that of a typical *Meconopsis*, only half as long as that of

M. Oliveriana, and with a distinct style. Not yet introduced into European gardens. Evidently perennial.

27. **Meconopsis Oliveriana**, Franch. & Prain. Rhizoma villosum; folia ovato-oblonga segmentis ovatis lobis obtusis vel subobtusis, caulibusque sparse strigosa; sepala glabra; capsula anguste cylindrica stylo perbrevi. Franch. & Prain, Journ. As. Soc. Beng., lxiv. 2. 312 (1895).

CHINA CENTRALIS et OCCIDENTALIS. Hupeh; in dumetis et umbrosis. Szechuen orientalis; in dumetis 12,000 p. s. m.

This species agrees in every character with *M. chelidonifolia* except as regards the fruit, which is in this species very like that of *Cathcartia villosa*, but only opens by short valves at apex, not all the way down as in a *Cathcartia*. Not yet introduced into European Gardens. Evidently perennial.

The *Chelidonifoliae* include only two species, which are so much alike that they can only be distinguished by their ripe capsules. These, however, are so dissimilar that while one has a style and stigma such as is characteristic of the majority of the species in the genus, the other has a sessile stigma exactly like that of *M. punicea* and *M. integrifolia*, or like that of *Cathcartia villosa*. In habit the two species are unlike any of the groups of *Meconopsis* except the *Cambricae*; in this respect they agree with *Cathcartia* § *Eucathcartia*. The capsules, however, open by the short apical valves characteristic of *Meconopsis*.

SPECIES EXCLUDENDAE.

MECONOPSIS BETONICIFOLIA, Franch., Pl. Delavay., 42, t. 12 (1889).
= **Cathcartia betonicifolia**, Prain.

This species has been accurately described by Franchet loc. cit., and the question as to whether the generic position assigned to the plant by Franchet, or that suggested by the writer, be the correct one turns on the nature of the ripe fruit, which as yet is unknown.

MECONOPSIS DIPHYLLA, DC., Syst. Veg., ii. 88 (1821).
= **Chelidonium diphyllum**, Michx, Fl. Bor. Am., i. 309 (1803).

MECONOPSIS PETIOLATA, DC., Syst. Veg., ii. 87 (1821).
= **Chelidonium diphyllum**, Michx.

2. CATHCARTIA.

The genus *Cathcartia* was founded in 1851 by Sir J. D. Hooker (Bot. Mag., t. 4596) to accommodate a yellow-flowered Himalayan Poppy collected by himself in Alpine Sikkim. The name perpetuates the memory of J. W. F. Cathcart, a member of the Indian Civil Service who, with the help of a native artist, prepared an important series of drawings of Sikkim plants. The validity of the genus has never been questioned, but its history during the past thirty years has been complicated by the reference to it of species that do not really belong. The first addition was suggested by

Maximowicz in 1876 when he described a Chinese Poppy as *Cathcartia integrifolia* (Mel. Biol., ix. 713). So far as the colour of the petals and the shape of the stigma are concerned, this plant, of which Maximowicz had not seen ripe fruits, is very like Hooker's original *C. villosa*. Subsequently further material with ripe capsules reached Paris, and in 1886 Franchet was able to show (Bull. Soc. Bot. Fr., xxxiii. 389) that Maximowicz's *C. integrifolia* is a genuine *Meconopsis*, the capsules opening as in other members of that genus by small apical chinks, and not, as in *C. villosa*, by valves that separate from the placental ribs to the base of the fruit. But in the place and at the time that Franchet made this rectification he himself published as *Cathcartiae* two species, *C. lancifolia* and *C. Delavayi*, which have proved to be species of *Meconopsis*. On the other hand, in 1889 Franchet published (Pl. Delavay., 42, t. 12), as *Meconopsis betonicifolia*, a species which the writer suspects may be a *Cathcartia*.

The writer was able in 1894 to study at Paris the abundant Chinese material of the natural family Papaveraceae in the Museum at the Jardin des Plantes, and owed much to the kindness with which Franchet put at his disposal the minute and extraordinary knowledge of the flora of south-western China which that generous and erudite botanist possessed. Franchet then pointed out that his original view as to the position of *C. lancifolia* and *C. Delavayi* required modification, and honoured the writer by permitting him to publish in 1895 (Journ. As. Soc. Beng., lxiv. 2. 311) the corrected determinations. As regards *Meconopsis* (or *Cathcartia*) *betonicifolia*, Franchet did not, however, think it advisable to modify his original view. This fact should be kept in mind by those who may hereafter have occasion to examine the plant in question. The actual position of this Chinese species, and of another from the eastern Himalaya which the writer has treated as a *Cathcartia*, *C. polygonoides*, can only be definitely settled when ripe fruits of both have been communicated. In the meantime it is certain that *Meconopsis betonicifolia* and *Cathcartia polygonoides* are very closely allied, and it is almost certain that both are very nearly related to yet another Himalayan species, *Cathcartia lyrata*, where the ripe capsules are known. In this last species the valves separate, as in *C. villosa*, from apex to base. For this reason the writer prefers, so long as the question as regards the other two is an open one, to place them beside *C. lyrata* and enumerate them in the genus *Cathcartia* rather than in the genus *Meconopsis*.

The genus *Cathcartia* is closely allied to the genus *Meconopsis*; the differential characters originally relied on were mainly the practical absence of a style in *Cathcartia* and the complete, in place of partial, separation of the valves from the placental ribs. But the character derived from the absence of a style is no longer differential, because there are at least three species of *Meconopsis—M. Oliveriana* in the group *Chelidonifoliae*, with

M. integrifolia and *M. punicea* in the group *Grandes*—where the depressed radiant stigma is situated, as in *Cathcartia villosa*, immediately on the vertex of the capsule. The introduction into *Cathcartia* of stylate species, if their valves do separate to the base, is no greater violation of its natural limits than is the retention in *Meconopsis* of the three non-stylate species mentioned.

The indumentum of *Cathcartia villosa* consists of barbellate hairs like those in the species of *Meconopsis* § *Polychaetia*; the hairs on the three stylate species are, on the other hand, simple, as in *Meconopsis* § *Eumeconopsis*. This character, in *Meconopsis*, appears to be of more consequence, from the taxonomic point of view, than the presence or absence of a style; it may be accepted as of equal importance in *Cathcartia*. Small as are the two groups which this character gives us, it seems therefore advisable to treat them as distinct sections. It has, indeed, to be pointed out that the only species of the three stylate *Cathcartias* with simple hairs of which we know the ripe fruit was considered by Sir G. King to deserve generic rank.

In habit the species of *Cathcartia* show considerable uniformity. All of them fall into the first of the three habit-series distinguishable within *Meconopsis*; they have slender non-scapose leafy stems with perennial rootstocks and few-flowered cymes, or even solitary flowers, terminating these leafy stems.

The distribution of the various species is as local as in the case of *Meconopsis*; *C. villosa* is known only from Sikkim and East Nepal; *C. lyrata* only from Sikkim; *C. polygonoides* only from Chumbi; and *C. betonicifolia* only from Yunnan.

All four species are truly alpine; none of them occur below 10,000 feet or go beyond 14,000 feet above sea-level; all are confined to the zone between 25° and 30° lat. N. As regards every feature of their distribution, therefore, the species of *Cathcartia* are in accord with the majority of the species of *Meconopsis*. The only one so far known in cultivation is *C. villosa*.

CATHCARTIA, HOOK. F.

Bot. Mag., t. 4596 (1851); Benth. & Hook. f., Gen. Pl., i. 52 (1862); Baill., Hist. des Plantes, iii. 140 (1872); Prantl & Kundig, Nat. Pflanzenfam., iii. 2. 141 (1889).

Sepala 2. Petala 4. Stamina ∞. Ovarii placentae 3–6 nerviformes vel plus minusve intrusae; stylus distinctus vel obsoletus; stigmatis clavati vel depresso-dilatati lobi decurrentes subcontigui vel radiantes divaricati placentis oppositi. Capsula oblonga vel anguste cylindracea vertice in stylum sensim vel sub stigmate subsessili abruptius attenuata, valvis ab apice ad basin usque placentas cum stigmate styloque persistentes nudantibus dehiscens.—Semina scrobiculata vel laevia raphe cristata vel nuda.—Herbae

perennantes succo flavo. Folia lobata crenatave. Flores longe pedunculati in cymas paucifloras racemiformes vel singuli caulem terminantes dispositi, speciosi, alabastris nutantibus.

Species 4, quarum 3 in Himalaya orientali, 1 in China austro-occidentali crescunt.

Genus in sectiones naturales 2 commode dividitur; scil.:—

§ **Eucathcartia.** Pilis setisve barbellatis densius indutae; flores lutei; stylus subnullus; stigmatis lobi radiantes divaricati.

§§ **Cumminsia.** Pilis simplicibus sparse obsitae; flores coerulei vel purpurascentes; stylus distinctus; stigmatis lobi decurrentes contigui.

CLAVIS SPECIERUM.

Flores lutei, maiusculi; stamina 32; stigma depresso-dilatatum lobis radiantibus divaricatis; folia dense villosa 1. *villosa.*

Flores purpurei vel coerulei; stigma clavatum lobis decurrentibus contiguis; folia sparse hirsuta:—

Folia ovato-lanceolata; petala margine integra:—

Flores majusculi; petala rotundata, obtusa; stamina 64 2. *betonicifolia.*

Flores minores; petala ovato-lanceolata, acuta; stamina 16 3. *polygonoides*

Folia integra hastata, vel lobata lyrato-pinnatifida; flores minores; petala ovato-lanceolata obtusa apice subfimbriata; stamina 16 4. *lyrata.*

§ I. EUCATHCARTIA. Herbae dense pilis setisve barbellatis villosae; folia radicalia plurima cordata lobata; flores lutei; capsula anguste cylindracea; stylus subnullus; stigma depresso-dilatatum lobis divaricatis radiantibus.

1. **Cathcartia villosa,** Hook. f. Folia molliter villosa, radicalia plurima, cordata 3–5-lobata lobis plus minusve incisis; flores maiusculi lutei in cymas racemiformes paucifloras caulem terminantes dispositi, pedicellis axillaribus; stamina 32; capsula anguste cylindracea; stylus subnullus; stigma latum depresso-dilatatum; semina scrobiculata raphe cristata. Hook. f., Bot. Mag., t. 4596 (1851); Fl. des Serres, vii. t. 686 (1851); Lem., Jard. Fleur., ii. t. 167 (1852); Hook. f. & Thoms., Flor. Ind., 254 (1855); Hook. f., Ill. Him. Pl., frontisp. (1855); Walp., Ann., iv. 175 (1857); Hook. f. & Thoms., Flor. Brit. Ind., i. 119 (1872); Prain, Journ. As. Soc. Beng., lxiv. 2. 325 (1895).

HIMALAYA ORIENTALIS. Nepal orientalis et Sikkim; in pratis alpinis, 10–12,000 p. s. m.

Habit of *Meconopsis Oliveriana* and *M. chelidonifolia,* but more hairy, with more numerous radical leaves, much larger flowers, and a capsule in shape like that of *Meconopsis Oliveriana* but larger, and with the valves separating to the base.

§ II. CUMMINSIA. Herbae sparse pilis simplicibus hirsutae; folia radicalia saepissime pauca margine crenata vel lyrata lobata; flores purpurei

vel coerulei; capsula ovata vel anguste cylindracea; stylus distinctus; stigma clavatum lobis decurrentibus contiguis. *Cumminsia*, King MSS. (gen.) in Herb. Calcutta et in Herb. Kew.

2. **Cathcartia betonicifolia,** Prain. Folia glabrescentia, radicalia numerosa, ovato-oblonga obtusa inciso-crenata; flores maiusculi purpurascentes in cymas racemiformes paucifloras caulem terminantes dispositi, pedicellis axillaribus; stamina 64; capsula (haud matura) oblongo-ovata in stylum distinctum sensim attenuata; stigma clavatum. *Meconopsis betonicifolia*, Franch., Pl. Delavay., 42, t. 12 (1889).

CHINA OCCIDENTALIS. Yunnan; in pratis alpinis, 10–12,000 p. s. m.

Habit of *Cathcartia villosa* but almost glabrous, with rather fewer radical leaves, and purplish flowers. The ripe capsule is not yet known.

3. **Cathcartia polygonoides,** Prain. Folia glabrescentia radicalia perpauca ovato-oblonga obtusa minopere inciso-crenata; flores parvuli purpurascentes vel albo-coerulescentes saepissime singuli caulem terminantes; stamina 16; capsula (haud matura) ovata in stylum distinctum sensim attenuata; stigma clavatum. Prain, Journ. As. Soc. Beng., lxiv. 2. 326 (1895); Ann. Roy. Bot. Gard. Calcutta, ix. 1. 6, t. 8 (1901).

HIMALAYA ORIENTALIS. Chumbi; in pratis alpinis, 10–12,000 p. s. m.

Exceedingly like *C. betonicifolia*, of which it might almost be considered a reduced form. It differs from that species in having narrower acute petals, fewer stamens, and hardly any radical leaves.

4. **Cathcartia lyrata,** Cumm. & Prain. Folia glabrescentia radicalia pauca varie hastata integra vel lobata lyrato-pinnatifida; flores parvuli purpurascentes vel coerulei, in cymas racemiformes paucifloras caulem terminantes dispositi vel singuli caulem terminantes; stamina 16; capsula anguste cylindracea in stylum distinctum sensim attenuata; stigma clavatum; semina laevia raphe ecristata. Cumm. & Prain, Journ. As. Soc. Beng., lxiv. 2. 325 (1895); Ann. Roy. Bot. Gard. Calcutta, ix. 1. 5, t. 7 (1901).

HIMALAYA ORIENTALIS. Sikkim; in pratis alpinis, 11–14,000 p. s. m.

Differs from *Cathcartia villosa* in its smaller size, different foliage with fewer radical leaves, smaller blue-purplish flowers with narrower petals erose at the apex, fewer stamens, distinct style, narrow stigma, and uncrested seeds.

SPECIES EXCLUDENDAE.

CATHCARTIA DELAVAYI, Franch., Bull. Soc. Bot. Fr, xxxiii. 390 (1886).
= **Meconopsis Delavayi,** Franch. ex Prain, Journ. As. Soc. Beng., lxiv. 2. 311 (1895).

CATHCARTIA INTEGRIFOLIA, Maxim., Bull. Ac. Imp. Petersb., xxiii. 310 (1876).

= **Meconopsis integrifolia**, Franch., Bull. Soc. Bot. Fr., xxxiii. 389 (1886).

CATHCARTIA LANCIFOLIA, Franch., Bull. Soc. Bot. Fr., xxxiii. 391 (1886).

= **Meconopsis lancifolia**, Franch. ex Prain, Journ. As. Soc. Beng., lxiv. 2. 311 (1895).

EXPLANATION OF PLATES XXIV AND XXV.

Illustrating Lieut.-Col. Prain's paper on *Meconopsis* and *Cathcartia*.

PLATE XXIV.

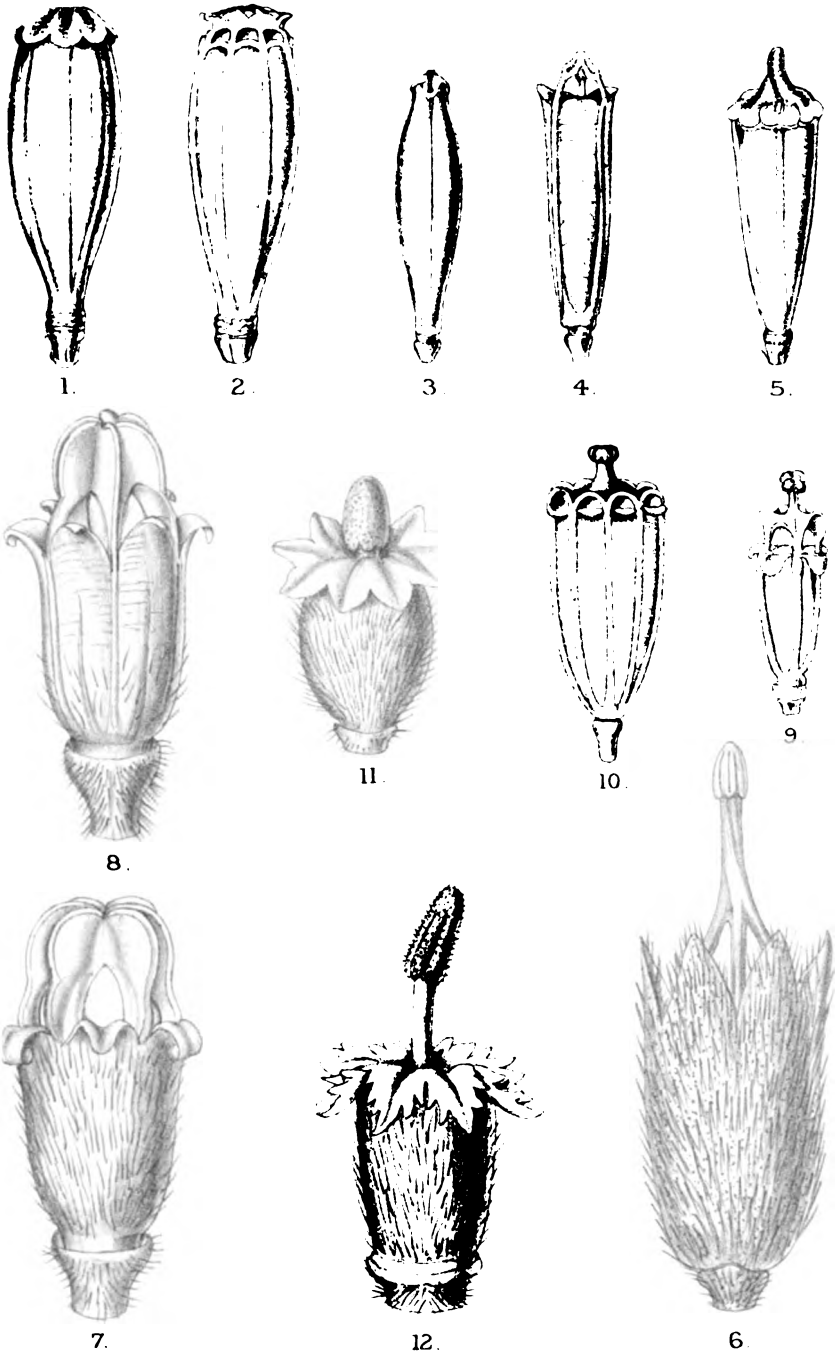
Capsules of *Papaver* and *Meconopsis*.

Figs. 1, 2. *Papaver dubium*, Linn. (Herb. Gay., 28). × 2.
Figs. 3, 4. *Papaver polychaetum*, Schott & Kotschy (Herb. Orient., Stapf.). × 2.
Fig. 5. *Papaver stylatum*, Boiss. & Bal. (Siehe, 96). × 2.
Fig. 6. *Meconopsis Wallichiana*, Hook. (Herb. Ind. Or. H. f. and T.). × 2.
Figs. 7, 8. *Meconopsis integrifolia*, Franch. (Herb. E. H. Wilson). Ad nat.
Fig. 9. *Meconopsis heterophylla*, Benth. (det. W. J. Hooker). × 2.
Fig. 10. *Meconopsis crassifolia*, Benth. (leg. C. F. Baker; det. Greene). × 2.
Fig. 11. *Meconopsis torquata*, Prain (leg. Walton). × 2.
Fig. 12. *Meconopsis discigera*, Prain (Cave, 1115 in Herb. Calcutt.). × 2.

PLATE XXV.

Meconopsis pseudointegrifolia.

Fig. 1. Habitus formaeque figura exempli *Meconopseos pseudointegrifoliae* vivi in horto botanico regio Kewense culti; magnopere reducti.
Fig. 2. Eiusdem folia, alabastra, flos apertus. Ad nat.
Fig. 3. Seta barbellata; magnopere aucta.
Fig. 4. Ovarium. × 2.



M. Smith del. Huth lith et imp

PRAIN—CAPSULES OF PAPAVER (Figs 1 to 5) AND MECONOPSIS (Figs 6 to 12)

M. Smith, del. Huth lith. et imp.

PRAIN — MECONOPSIS PSEUDOINTEGRIFOLIA.

The Anatomy of Lepidodendron aculeatum, Sternb.

BY

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With Plate XXVI, and Text-figures 1–3.

A DIFFICULTY which constantly confronts the palaeobotanist is that only in rare instances is he in a position to supplement an account of internal structure by a description of external features. The absence of external characters from petrified material and the lack of structure in specimens with well-preserved surface features necessitate the use of two series of specific names: the same plant must frequently be known under two designations, one having reference to anatomical structure, and the other to external features.

The late Professor Williamson wrote in his second Memoir 'On the Organization of the Fossil Plants of the Coal-Measures'[1]: 'I am satisfied that all attempts to apply specific names to the plants of the Coal-Measures can but be provisional, until we learn more than we at present know of the effects of age upon their form and organization. Still, though they may not have any permanent value, such names are necessary for working purposes.' To those botanists who worked with Professor Williamson this statement affords but a partial reflection of the vigorous protests against the institution of specific names which he frequently made in conversation.

In the case of several species of Lepidodendreae founded on anatomical characters we are unable to give a satisfactory account of the external characters: it is not only a question of correlating species founded respectively on impressions and petrifications, but the choice of a generic name may be a serious difficulty.

The two genera *Lepidodendron* and *Lepidophloios* are, as a rule, easy to distinguish by the form of the leaf-cushions and leaf-scars, but we are not in a position to assign with confidence a petrified lepidodendroid stem, on anatomical evidence alone, to one or other of these genera. In 1894,

[1] Williamson ('72), p. 310.

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Williamson wrote:—'It appears to me that much uncertainty exists amongst Palaeobotanists respecting the structures that distinguish *Lepidodendron* from *Lepidophloios*[1].' The specimen described below adds point to this opinion.

A few examples of lepidodendroid stems founded on anatomical characters serve to illustrate the grounds on which one or other of these two generic names has been used.

The specimens described by Binney, in 1862, as *Sigillaria vascularis* and *Lepidodendron vasculare*[2] were afterwards recognized as one and the same type. Carruthers.[3] identified the species, founded on anatomical characters, with *Lepidodendron selaginoides* Sternb., but the nature of the evidence on which the anatomical structure of *Lepidodendron vasculare* was referred to Sternberg's species, founded on external characters, is not stated. On the strength of Mr. Carruthers' identification we may regard *Lepidodendron vasculare*, Binney, as a well-defined anatomical type associated in some cases, though not necessarily in all, with the external features of *Lepidodendron selaginoides*, Sternb., which is a synonym of *L. Sternbergii*, Brongn.[4]. The common practice of speaking of Binney's type as *L. selaginoides* is, I think, unfortunate: though a comparatively small point, the name *L. vasculare* has the advantage of not committing us to the inference that all stems with the type of structure associated with Binney's species necessarily agree in the form of the leaf-cushions with the plant named by Brongniart *L. Sternbergii*, and by Sternberg *L. selaginoides*.

The species described by Witham[5] as *Lepidodendron Harcourtii* has been investigated by several botanists since 1832[6]. Some of the specimens originally included by Williamson in Witham's species were subsequently recognized by him as distinct, and referred to a new species *Lepidodendron fuliginosum*[7]; for this type Solms-Laubach proposed the name *L. Williamsoni*[8], but the former designation has been generally adopted. The true *Lepidodendron Harcourtii* is considered by Kidston to be a species of the genus *Lepidophloios* as 'it has all the peculiarities'[9] of that genus, but no satisfactory evidence has been adduced as to the external features of Witham's anatomical species.

In 1890 Messrs. Cash and Lomax[10] mentioned a petrified stem in their possession—'whose external surface is marked by tolerably well-preserved characters, which leave no doubt that it must be referred to the genus *Lepidophloios* as defined by Sternberg'—exhibiting the type of structure

[1] Williamson ('94), pp. 423, 424, footnote.
[2] Binney ('62).
[3] Carruthers ('69), p. 179.
[4] Kidston ('86), p. 151.
[5] Witham ('32).
[6] Bertrand ('91) has given a comprehensive historical sketch of our knowledge of *L. Harcourtii* in his Memoir on the anatomy of the species.
[7] Williamson ('87).
[8] Solms-Laubach ('87).
[9] Kidston ('01), p. 59.
[10] Cash and Lomax ('90).

designated by Williamson *Lepidodendron fuliginosum*. This identification has since been confirmed by Kidston [1] and by Weiss [2].

The large stems from Arran named by Williamson [3] *Lepidodendron Wunschianum* have been described as bearing Halonial branches, and for this reason they have been referred to the genus *Lepidophloios* [4]. It has been suggested that the Arran species may be specifically identical with *Lepidodendron Harcourtii* [5], but the evidence available does not justify a positive statement as to identity.

The petrified specimens from the Lower Carboniferous beds of Pettycur, near Burntisland, on which Williamson founded the species *Lepidodendron brevifolium* [6], in all probability possessed the external characters of *L. Veltheimianum* [7]. A recent discovery by Mr. Lomax enables us to refer Williamson's type *Lepidodendron mundum* [8] to the genus *Bothrodendron*, and Dr. Scott has in his possession a specimen with the external characters of *L. obovatum* showing well-preserved internal structure [9].

Reference may be made to *Lepidophloios acadianus*, Daws., and to *Lepidodendron Derbyi*, Ren., as additional examples of lepidodendroid plants in which internal structure and external features occur together. Sir William Dawson [10] described *Lepidophloios acadianus* in 1866 from the Canadian Coal-Measures, and an additional account of the species was published by the same author in 1897.

An example of this species described by Dawson as a Halonial branch bearing two rows of cone-scars may be compared with the specimen recently dealt with by Weiss [11], but the anatomical preservation of the Canadian plant, as represented in the somewhat rough sketches in the earlier paper and in the microphotographs by Prof. Penhallow in the later account, is too imperfect to enable us to attempt a satisfactory comparison with British anatomical types.

Mr. Kidston [12] regards *Lepidophloios acadianus* as specifically identical with *L. laricinus*, Sternb.

In 1890 M. Renault [13] proposed the name *Lycopodiopsis Derbyi* for a Brazilian specimen exhibiting external features and internal structure; he described the anatomy of the central cylinder as differing in important characters from that of the *Lepidodendron* type. The acquisition of additional specimens from Brazil enabled M. Zeiller [14] to modify Renault's interpretation, and to identify the species as a true *Lepidodendron* allied

[1] Kidston ('93), p. 343; ('01), p. 58.
[2] Weiss ('08), p. 218.
[3] Williamson ('72[2]).
[4] Kidston ('01), p. 59.
[5] Seward and Hill ('00), p. 921.
[6] Williamson (72[3]), p. 310.
[7] Kidston ('01), p. 60.
[8] Williamson ('89).
[9] I am indebted to Dr. Scott for generously lending me his specimen of *L. obovatum* for examination. [Since this was written, Dr. Scott has published a description of his specimen. See *Annals*, Vol. XX, p. 317, 1906.]
[10] Dawson ('66), ('97).
[11] Weiss ('08).
[12] Kidston ('86).
[13] Renault ('90).
[14] Zeiller ('98).

anatomically to *L. Harcourtii*, and in the form of the leaf-cushions possibly identical with *L. Pedroanum*, Carr.[1]

Description of Specimen. The fossil which forms the subject of the following description has long been in the collection of the Cambridge Botany School, and several years ago Mr. C. A. Barber, then University Demonstrator, had a single transverse section cut. On re-examining the specimen and the section I was surprised to find the preservation of the tissues much more satisfactory than my recollection of it led me to expect. I am unable to give any information as to the history of the fossil; it was undoubtedly obtained from the English Coal-Measures, but there is no record of the locality. The general appearance of the calcified tissues presents a striking resemblance to that of some sections in the Binney Collection in the Sedgwick Museum, Cambridge, obtained from the clay-ironstone of the Coal-Measures near Dudley [2].

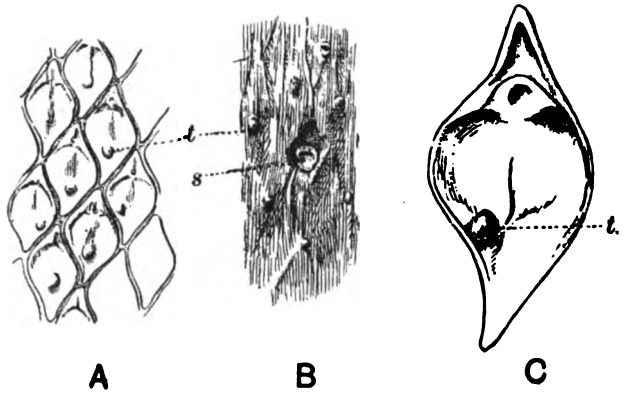

FIG. 1.

The piece of stem is 6·8 cm. long, and has a diameter of 4·8 × 4·5 cm. A thin layer of coal, approximately ·5 mm. thick, covers a portion of the surface. Part of the surface (Pl. XXVI, Fig. 1; text-fig. 1, A. C) is almost intact: the leaf-cushions, 1·5 cm. long, are prolonged both upwards and downwards in tapered and slightly curved terminations. A ligular pit may be recognized on some of the cushions, as also the position of the leaf-scars, but the preservation is not sufficiently good to enable one to make out the parichnos-scars. The cushions are flat or slightly depressed; on each a small tubercle (Text-fig. 1, *t*) forms a conspicuous feature, occurring either on the median line or near one edge in the lower third of the cushion region. These scars probably mark the position of leaf-traces which the shrinkage and depression of the tissues have rendered apparent on the surface of the stem. For the most part the surface has suffered partial decortication:

[1] Carruthers ('69[2]).

[2] Seward ('99).

the depression shown in Text-fig. 1, B. *s*, which looks like a small branch-scar, appears on examination of the tissues to be the result of a wound. The dark tissues seen at C, Fig. 5, Pl. XXVI, a section cut through the scar (Text-fig. 1, B. *s*), marks the position of the partially destroyed cortex and wound periderm.

The external characters point to *Lepidodendron aculeatum*, Sternb., as the species with which the form of the leaf-cushions agrees most closely. There can at least be no doubt as to the genus to which the fragment belongs. The geological range of *L. aculeatum* in Britain is stated by Kidston[1] to be from the Millstone Grit to the Upper Coal-Measures.

The transverse section, represented natural size in Fig. 5, Pl. XXVI, illustrates the imperfect state of preservation of the slightly excentric stele, the tissues of which have been considerably shattered, though in places the structure is very clearly shown. The largest diameter of the somewhat flattened stele, measured from the outer edge of the xylem, reaches 1 cm. There is no trace of any secondary xylem; the primary xylem consists of a tube of scalariform tracheids, usually about six tracheids broad, with narrow protoxylem-elements at the outer edge forming fairly prominent teeth of the single or double type (Text-fig. 2, *x*) as in *Lepidodendron Harcourtii* and *L. fuliginosum*.

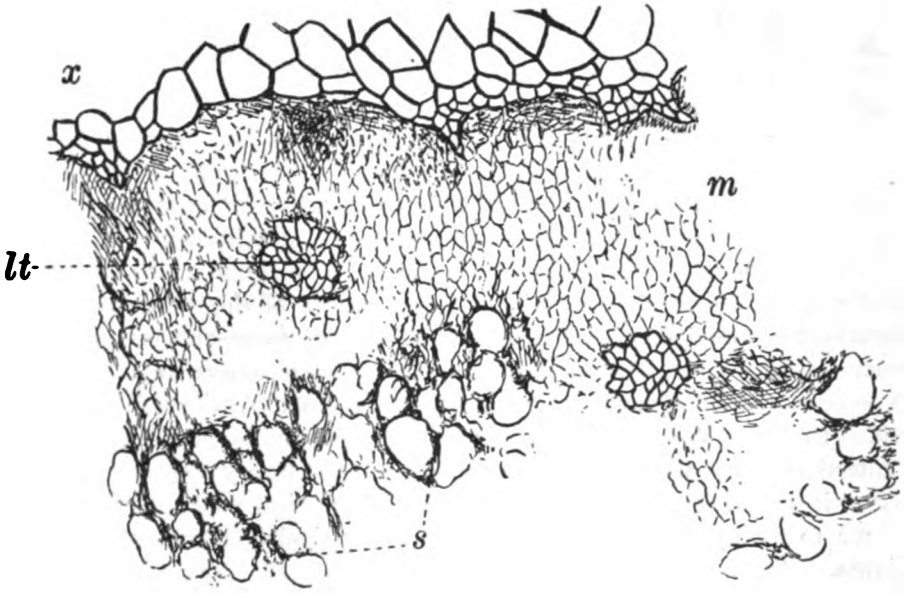

FIG. 2.

Such of the pith-tissue as remains exhibits the histological features usually met with in this region of lepidodendroid stems. The zone between

[1] Kidston ('94), p. 251. For figures of this species, see Zeiller ('88), Pl. LXV. Figs. 1–7; also Kidston ('01), p. 44, and Zalessky ('04).

the outer edge of the wood and the inner cortex has suffered considerably, either from disorganization of the tissues before petrification, or perhaps to a large extent from the effects of secondary crystallization. In the portion shown in Text-fig. 2, the preservation is exceptionally good; the xylem is succeeded externally by a broad band of small-celled parenchyma (*m*) which is darker and denser along its inner margin. This is the tissue which previously has been described as the meristematic zone [1]; it is composed exclusively of short parenchymatous cells, and in other examples of Lepidodendron it is known to be the seat of secondary growth. In the portion of this zone seen in Text-fig. 2, there are no indications of meristematic activity, but a few radially elongated cells occur in other parts of the same section which are identical in form with the elements figured in some of the specimens of *L. fuliginosum* from the Binney Collection.

The leaf-traces follow an almost vertical course in the meristematic zone, and they pass through the cortical region at an unusually small angle (Text-fig. 3, *lt*). The xylem-strand as seen at *lt*, in Text-fig. 2, is approximately circular in outline with the smallest tracheids in a more or less central position. The broad parenchymatous zone *m* is succeeded by a slightly narrower band composed of large clear spaces interspersed with very dark lines and patches of disorganized smaller cells. This tissue is preserved in a few patches only, but it is sufficiently distinct in the portion represented in Text-fig. 2, *s* to demonstrate its identity with the tissue which I formerly described as the secretory zone [2], but which Professor Weiss [3] prefers to designate phloem. The nature of this tissue has been described in previous accounts of lepidodendroid stems, and reasons have been brought forward against my objection to recognize it as phloem. A recent examination of several sections of *Lepidodendron fuliginosum*, which Professor Weiss generously sent to me from the Manchester Museum Collection, does not lead me to modify views already expressed. The tissue in question does not exhibit such histological characters as seem to me to justify the title of phloem, as understood in the case of recent plants.

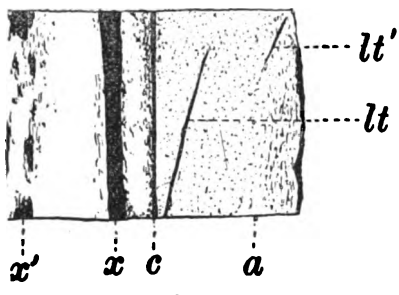

FIG. 3.

A band of compact parenchyma composed of small and rather dark elements abuts on the secretory zone; this is the inner cortex (Text-fig. 3, *c*), and it appears to be identical in structure with the corresponding region in other lepidodendroid stems. The boundary between the inner

[1] Seward ('99), ('02). [2] Seward, *loc. cit.* [3] Weiss ('01), ('03).

and middle cortex is clearly defined by the junction of the vertical rows of the short cells of the former with the loose tissue of irregularly branched and hypha-like cells of the latter, which tend to assume a horizontal rather than a vertical direction.

Numerous leaf-traces in slightly oblique transverse section occur in the middle cortex. A leaf-trace as seen in this region (Fig. 4, Pl. XXVI) consists of a somewhat tangentially elongated xylem-strand (*x*) separated by a few layers of delicate elongated and narrow cells (*b*) from a patch of dark disorganized tissue in continuity with the secretory zone. The whole trace is enclosed by a few layers of parenchymatous cells (peridesm), of which those on the adaxial side often assume a radially elongated form (Fig. 4, *p*). The structure of a leaf-trace is shown in longitudinal section in Fig. 3, Pl. XXVI. In the actual specimen the spiral protoxylem-elements are clearly seen, while the scalariform metaxylem-tracheids show a slight tendency towards a reticulate form of pitting. The xylem is shown at *x* and the disorganized cells of the secretory zone at *s* in Fig. 3, Pl. XXVI. The contrast between the compact peridesm (*p*) and the loose cortex is seen at *p. c.*

The clear line near the surface of the transverse section, reproduced in Fig. 5, Pl. XXVI, represents a break in the tissue filled with mineral substance, immediately internal to the sharply defined junction between the outer edge of the middle and the inner edge of the firmer and much more compact outer cortex.

The cells at the inner edge of the outer cortex are short and rather flat and in longitudinal sections exhibit a fairly regular vertical arrangement, but they gradually assume a more elongated and prosenchymatous form towards the outer surface of the stem. No signs of phelloderm can be detected, nor are there any indications of the secretory canals which often occur immediately internal to the secondary cortical tissue of other lepidodendroid stems. Fig. 6, Pl. XXVI represents a portion of the outer edge of a transverse section. The superficial tissue has been converted into a patch of pure coal, which sends irregular threads between the disorganized cortical cells. The gradual passage from coal to well-preserved tissue reminds one of the appearance presented by sections of silicified Liassic wood partially converted into jet[1]. It may be that the branch under consideration had not reached the stage of producing a phelloderm, or possibly the conversion into coal of the superficial tissue has destroyed the results of phellogen activity.

Fig. 2, Pl. XXVI shows a leaf-trace in the outer cortex accompanied by a large crescentic parichnos which is simply an accompanying strand of middle cortex. In structure the leaf-traces appear to be identical with those described in sections from the Binney Collection referred to, *Lepidophloios fuliginosus*[2]. The boundary between the parichnos and outer

[1] Seward ('04), p. 66, Pl. VIII, Figs. 1 and 2.

[2] Seward ('99).

cortical tissue is seen at *a*, Fig. 2, Pl. XXVI; the secretory strand and xylem with the intervening cambiform cells are shown at *s*, *x* and *b*.

The two dark strips extending from the surface of the section seen in Fig. 5, *c*, and converging in the inner cortex consist of partially destroyed tissue bounded externally by cortical cells characterized by the presence of numerous secondary septa parallel to the wounded surfaces. The area between the two dark lines in the cortex is partly occupied by shrunken and isolated cells, which appear to have fallen apart as the result of the destruction of the middle lamellae. The xylem-ring internal to the injured region exhibits the normal structure.

The anatomy of the specimen (Fig. 1) possessing the surface characters of *Lepidodendron aculeatum* exhibits an exceedingly close agreement with that type of structure which it has been customary to describe as *Lepidophloios fuliginosus*. So far as I am aware the only reference to the structure of *Lepidodendron aculeatum* previously published is by Prof. Bertrand [1], who has mentioned the occurrence of petrified portions of suberous tissue in the nodules of Hardinghen, which are probably referable to this species. It has been pointed out by Weiss that the leaf-traces in the stem described by him as a biseriate Halonia, and referred on anatomical grounds to *L. fuliginosus*, pursue an almost horizontal course in the middle cortical region [2]: this is also the case in sections of other specimens of the same type which I have had an opportunity of examining. The steeply ascending course of the traces in the branch of *Lepidodendron aculeatum* (Text-fig. 3) constitutes a distinguishing feature—of how much value it is difficult to say. A comparison of the previously published figures of small branches of *Lepidodendron fuliginosum* with those given in this paper demonstrates a striking similarity which, with the exception of the course of the leaf-traces, seems to amount to identity. The age of the branch does not enable us to say anything as to the nature of the secondary xylem, which in older specimens constitutes a characteristic peculiarity of *L. fuliginosum*.

Such evidence as is available would seem to point to the absence of trustworthy criteria enabling us to separate, on anatomical grounds, *Lepidophloios* and *Lepidodendron*. Weiss refers his biseriate Halonia to the former genus 'on the strength of its internal structure' [3], but it is questionable whether the present state of our knowledge of lepidodendroid anatomy is sufficiently accurate to render this argument valid. Mr. Kidston, [4] who

[1] Bertrand, Cornaille and Hovelacque ('97), p. 491; Bertrand ('99), p. 391.

[2] Weiss ('08), p. 223.

[3] Weiss ('08), p. 220. It should be mentioned that Prof. Weiss (*loc. cit.*) adds:—'as, however, an identification based solely on the internal structure might be disputed by some, I would seek to strengthen my conclusion by evidence from specimens showing external markings which can be identified with *Lepidophloios* and which at the same time possess only two rows of tubercles.'

[4] Kidston ('05), p. 538.

dissents from Prof. Weiss's interpretation of the tuberculated branch, expresses the opinion that the anatomical characters are not identical with those of the true *Lepidodendron fuliginosum*, though he recognizes that Weiss's specimen belongs to the same *type* of structure as the vascular axis of that species. The differences mentioned by Kidston do not appear to me of sufficient importance to serve as an objection to the use of the term *L. fuliginosum* on anatomical grounds; but the more important point is, the existence of this type of anatomical structure does not necessarily imply that the stem exhibiting it possessed the surface features of *Lepidophloios*. Mr. Kidston regards the tuberculated specimen as a fertile branch of *Sigillaria discophora* (*Ulodendron minus*). It would lead us too far afield to enter into the arguments for or against the reference of the fertile branch to *Lepidophloios*, but the foregoing description justifies the view that on anatomical evidence alone we cannot in the present state of our knowledge safely assume that the type of structure described by Williamson as *Lepidodendron fuliginosum* is the exclusive possession of *Lepidophloios*. Dr. Scott gave expression to this view when he wrote:—'So far as is known, however, there is no constant difference in internal structure between *Lepidophloios* and *Lepidodendron*[1].'

Without discussing the value of the presence of Halonial tubercles as a mark of distinction between *Lepidophloios* and *Lepidodendron*, I submit that it is better to refrain from attempts to separate these two genera on purely anatomical evidence. The fragmentary nature of our material and the almost constant absence of external features in the case of petrified specimens are obstacles in the way of satisfactory identification and correlation; it is better to recognize the limitations imposed by imperfect knowledge, and to rest content with the application of specific terms to anatomical types without regard to those rare cases in which external and internal characters are supplied by the same specimen. The same anatomical type, or rather what the fragments at our disposal lead us to regard as the same type, does not necessarily imply identity in external features. Our acquaintance with the anatomy of Palaeozoic Lepidodendreae is much too meagre and superficial to enable us to judge of the degree of correspondence between the two kinds of characters available for specific definition. I would therefore speak of the specimen described above as belonging to the type *Lepidodendron fuliginosum*, a type of structure which occurs in association with *Lepidophloios* as well as with *Lepidodendron* leaf-cushions.

The present state of our ignorance on many histological points connected with the Lepidodendreae as well as in regard to grosser anatomical characters affords a strong plea for a thorough comparative examination of the Palaeozoic Lycopods.

[1] Scott ('00), p. 123.

In his address to the Botanical Section of the British Association, in 1896, Dr. Scott said:—'We are now in possession of a magnificent mass of data for the morphology of the Palaeozoic Lycopods, and have perhaps hardly yet realized the richness of our material. I refer more especially to specimens with structure, on which, here as elsewhere, the scientific knowledge of fossil plants primarily depends[1].' The revision of this material, as regards both the organization as well as the extension of the data, is an urgent need.

[1] Scott ('96).

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EXPLANATION OF PLATE XXVI.

Illustrating Mr. Seward's paper on *Lepidodendron aculeatum*.

Fig. 1. Portion of the petrified specimen showing the leaf-cushions. (Nat. size.)

Fig. 2. Leaf-trace as seen in transverse section, cut from the specimen shown in Fig. 1, in the outer cortex.

a = junction between parichnos and cortex.
x = xylem.
s = secretory strand.
b = cambiform cells.

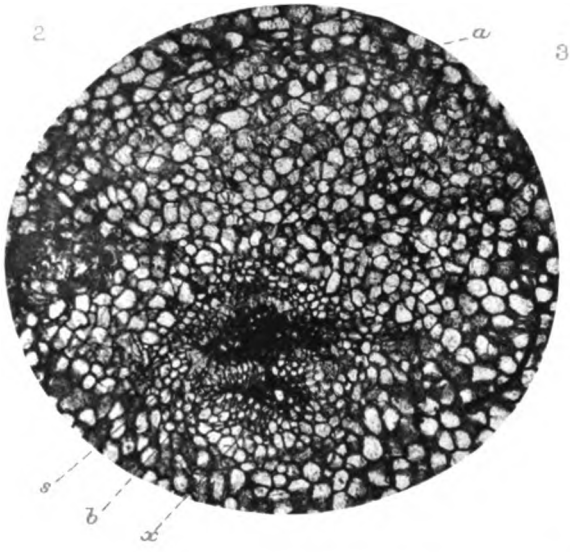
Fig. 3. Leaf-trace in longitudinal section.

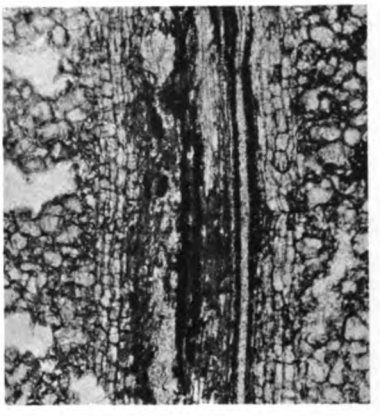
c = middle cortex of stem.
p = peridesm.
s = secretory tissue.
x = xylem.

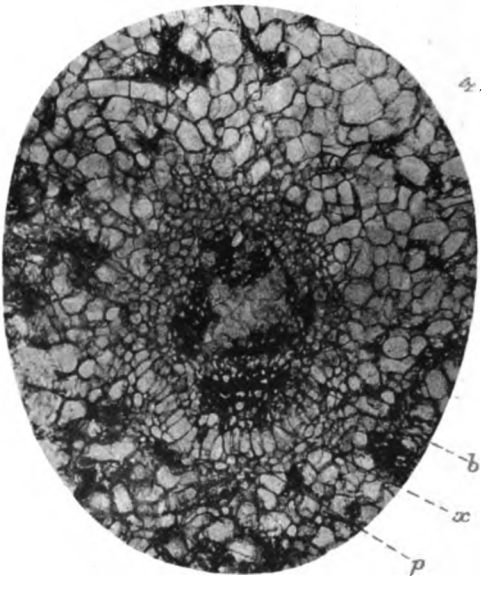
Fig. 4. Leaf-trace as seen in transverse section of the stem (Fig. 1) in the middle cortical region. Lettering as in Fig. 2.

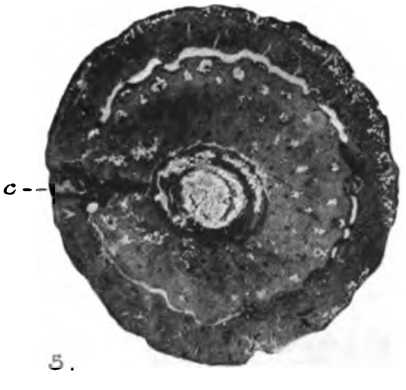
Fig. 5. Transverse section of the stem represented in Fig. 1, cut through the scar *s* shown in Text-fig. 1, B.

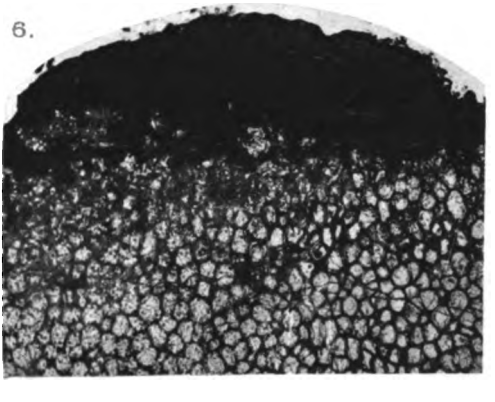
Fig. 6. Portion of leaf-cushion converted into coal as seen at the edge of a transverse section.











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SEWARD — LEPIDODENDRON ACULEATUM

The Wound Reactions of Brachyphyllum[1].

BY

EDWARD C. JEFFREY.

Assistant Professor of Botany in Harvard University.

With Plates XXVII and XXVIII.

THE genus *Brachyphyllum* was established by Brongniart for the leafy branches of a Jurassic coniferous plant of doubtful affinities (Prod. Hist. Vég. Fossiles, p. 109, 1828). Saporta, who subsequently described a number of species of the genus (Plantes Jurassiques, vol. iii, 1884), placed it with the Araucarineae. This type of foliar shoot from the Cretaceous and Jurassic deposits of different parts of the world has been referred by various authors under several generic appellations to the Araucarineae, Cupressineae, and Sequoiineae, with perhaps the weight of authority inclining towards the last attribution. The present writer, in collaboration with Dr. Arthur Hollick of the New York Botanic Garden, on the basis of well preserved material, has been able to settle finally the systematic position of these interesting and omnipresent relics from the Jurassic and Cretaceous strata, from the investigation of internal structure. The anatomical features of *Brachyphyllum*, as exemplified by the North American species *B. macrocarpum*, Newberry, are such that there can now be no doubt as to its Araucarian affinities (Affinities of certain Cretaceous Plant remains commonly referred to the genera Dammara and Brachyphyllum, American Naturalist, vol. xl, pp. 189–215, March, 1906). In the article just cited, it has been demonstrated that *Brachyphyllum*, although presenting undoubted Araucarian features, differed markedly from existing and many extinct Araucarineae, both in the structure and wound reactions of its wood. These features are to be farther discussed in the present article, because they appear to be of considerable importance not only from the standpoint of the identification of lignites and mineralized woods, which are the remains of *Brachyphyllum*, but also from that of the general question of the affinities and phylogenetic history of the Araucarineae. The present writer has now in his possession a considerable amount of fossil

[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 7.

[Annals of Botany, Vol. XX. No. LXXX. October, 1906.]

woods belonging to the genus *Brachyphyllum*, which has come from Cretaceous deposits of somewhat extended geographical and stratigraphical range, on the eastern coast of the United States. For this reason it becomes possible to treat the subject of the wound reactions of the wood of this genus with some degree of thoroughness.

A feature which makes it possible to distinguish at once a well preserved specimen of the wood of *Brachyphyllum* from that of any living representative of the Araucarineae or fossil forms more nearly allied to these, is the absence of resiniferous elements in the wood, other than those found in the medullary rays. Photograph 1, Plate XXVII, which is of a remarkably well preserved lignite from the Androvette pit, Kreischerville, Staten Island, N. Y., illustrates the truth of this statement. Although there are three annual rings present in the field of the photomicrograph, it is impossible even by the use of a magnifying lens to distinguish the presence of any resinous elements, such as occur in numbers in the wood of either of the living Araucarian genera *Agathis* and *Araucaria*. A somewhat extensive study of both longitudinal and transverse sections of the wood of *Brachyphyllum* has failed to reveal the presence of resiniferous elements of any kind in the normal wood of this genus. In this normal absence of resiniferous elements in the wood, *Brachyphyllum* resembles the older Gymnospermous groups, such as the Cordaitales, the Cycadales, the Pteridospermae and their allies, not to mention the fossil Lycopodiales and Equisetales, in so far as these possessed secondary wood. In this respect too it also presents a striking degree of similarity to the very ancient although still flourishing coniferous genus *Pinus*, for in the pines there are no parenchymatous elements in the wood, other than those which surround the resin canals.

Photograph 2, Plate XXVII, represents a part of a radial section of the same material, highly magnified. The radial pits of the tracheids occur in a single row, and are flattened above and below by mutual contact. The fact that in *Brachyphyllum* the radial pits ordinarily occur in a single row only, is probably due to the xerophytic habit of the genus, which is very marked. Very rarely the pits are in a double row in the ends of the tracheids, and then they alternate in the manner typical for the Araucarineae. Such a case of alternation has been figured in the first article, already cited above. The mutual flattening of the bordered pits of the tracheids is a sufficient diagnostic of Araucarian affinities, where the radial pits occur in but a single row. Another pronounced Araucarian feature is the presence of numerous crowded pits on the lateral walls of the cells of the rays. As this character has likewise been figured in the article referred to above, it need not be further discussed at the present time (*op. cit.*, Pl. 5, Fig. 2).

The same block of lignite, which supplied the sections illustrated in the two photographs described above, showed at one end evidence of

a healed wound. The fact that the material was partially carbonized, especially in the region of the wound, made it difficult to secure satisfactorily thin sections through the traumatic region. This was regrettable on account of the fact that the black opacity of the tissues made thin sections particularly desirable. However, the partial burning of the material has on the whole been an advantage, for it has resulted in a superb condition of preservation. Photograph 3, Plate XXVII, shows a section through the partially callused wound, under a low magnification. Two folds of traumatic wood are seen overlapping the injured surface in the manner characteristic of ligneous wounds. Photograph 4, Plate XXVII, represents a view of a section either on a lower or higher plane than that shown in the last photograph. It is of course not possible to decide which alternative is the correct one, in view of the fragmentary condition of the piece of wood. The wound is closed over in the centre, at this level, as may be seen by comparing the two narrow annual rings, most clearly discernable on the left of the wound, with the two similar rings in the foregoing photograph. By the use of a lens, it may be observed, that stretching away tangentially on either side of the wound is a row of apertures in the wood. These are traumatic resin-canals. Photograph 5, Plate XXVII, shows the right margin of the wound in photograph 4, much more highly magnified. Towards the left of this photograph is a mass of resiniferous parenchyma, such as is found in connexion with healing wounds in nearly all Conifers. To the right of this mass of resinous parenchyma extends a tangential series of resin-canals. Photograph 6, Plate XXVII, shows the continuation of this series of traumatic canals, beginning about the centre of the former photograph. On the left of photograph 6 may be recognized the same canals as are found in the centre of photograph 5. These series of canals stretch to the extreme margins of the fragment of wood. Photograph 7, Plate XXVII, shows a row of canals from a plane of section so far removed from the actual wound, that there is scarcely any evidence of traumatic disturbance in the arrangement of the elements of the wood. In this photograph it is possible to distinguish, that although there are no resinous elements in the wood proper, dark coloured cells surround the traumatic resin canals. Photograph 8, Plate XXVII, shows one of the larger canals highly magnified. The contents of the resiniferous cells surrounding the canal are so dark, that they present no actinic contrast with the almost black walls of the cells themselves. In photographs 7 and 8 it is possible to make out that the row of traumatic resin-canals occur in the autumnal wood of the specimen under discussion. Photograph 9, Plate XXVII, is of a longitudinal section of the same piece of lignite, showing a traumatic canal in longitudinal section. The canal is obviously lined by dark hued cells and is constricted at intervals. The latter feature is found in the case of traumatic and even normal resin-canals in the Abietineae. The canals are jacketed not only by

parenchyma cells, but also by septate tracheids, such as have been described by Penhallow and Conwentz in the case of the normal and traumatic resin-canals of living and fossil species of *Pinus* and other Abietineous genera, as well as in the traumatic resin-canals of *Sequoia*. Photograph 10, Plate XXVII, shows a double row of traumatic resin-canals in another specimen of the wood of *Brachyphyllum* from Kreischerville, Staten Island, which was not charred in any way, and is consequently much less well preserved than is the case with the material in the foregoing photographs. The specimen in question is of some interest however, since it shows a double row of traumatic resin-canals in the same annual ring. This feature appears to be rare, although not infrequently rows of traumatic canals occur in successive, although not consecutive, annual rings. In none of the material which has been gathered have horizontal canals been found, connecting the rows of vertical ones, such as are present in the genus *Cedrus* among the Abietineae (Comp. Anat. and Phylog. of the Coniferales, 2; The Abietineae, Bost. Soc. Nat. Hist. Memoirs, vol. vi, No. I), and in a fossil *Sequoia* (A fossil Sequoia from the Sierra Nevada, Bot. Gazette, 38, 321–332, Nov., 1904).

The traumatic phenomena described in the foregoing paragraphs were found in fragments of lignite which, by comparison with the woody tissues of associated, well preserved branches of *Brachyphyllum macrocarpum*, were inferred to be portions of the wood of this or an allied species. It has, however, fortunately not been necessary to rest the case on inference alone. On sectioning one well preserved, partially carbonized branch of *B. macrocarpum*, Newberry, it was found that it had suffered injury, and that a large amount of traumatic parenchyma was present in the wood, in some cases enclosing traumatic resin-canals. The small size of the branch and the limited amount of woody tissue are doubtless responsible for the fact that the traumatic canals were not more abundant, since similar conditions are present in small wounded branches of the living Abietineae. Photograph 11, Plate XXVII, shows a general view of the central portion of a transverse section of the specimen of *Brachyphyllum* just mentioned. The fibro-vascular bundles on account of the youth and small size of the branch are still separate from each other, and have not become united into a continuous woody cylinder as in older stems of this genus. A parenchymatous stripe can be seen running through the outer half of the wood in most of the bundles shown in the photograph. This stripe in the case of a large bundle near the centre of the photograph encloses two resin-canals. Photograph 12, Plate XXVII, shows this bundle more highly magnified. On the left is a resin-duct surrounded by a layer of dark parenchyma, which has very largely collapsed. Farther to the right is another resin-canal less perfectly preserved. The two canals are situated in the parenchymatous stripe of traumatic tissue, which crosses the wood tangentially. It is thus apparent that traumatic resin-canals of the same type, as are

found abundantly in isolated fragments of wood possessing the characters of that present in leafy and determinable branches of *Brachyphyllum*, in this instance occur in the wood of an authentic branch itself. The diagnosis is thus placed beyond any reasonable doubt, since it is extremely improbable that two different extinct genera of Araucarineous remains should present this very remarkable traumatic reaction.

It becomes necessary at this stage to compare the traumatic reactions of the living genera of the Araucarineae with those of the extinct Mesozoic genus *Brachyphyllum*. Photograph 13, Plate XXVIII, shows a portion of the edge of a healed wound in *Agathis alba*, material of which was very kindly sent by the Director of the Botanic Gardens at Buitenzorg, Java. It will be seen from the photograph, that although there is a considerable amount of callus formed on the margin of the wound, there is no indication whatever of the presence of traumatic resin-canals such as invariably appear in connexion with healed wounds in *Brachyphyllum*, so far as has been observed. Through the great kindness of Dr. Treub, Director of the Botanic Garden at Buitenzorg, Dr. Maiden, Director of the Botanic Garden at Sydney, N.S.W., Dr. L. Cockayne, of Christchurch, New Zealand, and Professor G. L. Goodale, Director of the Botanic Garden of this University, the writer has had the opportunity of examining the traumatic reactions of a considerable number of species of *Agathis* and *Araucaria* of wide geographical distribution. In all the cases yet studied, the conditions resulting from wounds are substantially the same as those shown in photograph 13. It is not proposed to discuss this matter farther at the present time, as it will be sufficiently considered in a future memoir on the living Araucarineae. One feature of healing wounds in the existing Araucarineae is, however, worthy of present notice, viz. the fact that there is an abundant formation of mucilage in connexion with the wound, similar to that found normally with the resin, in their cortical resin-canals. This mucilage generally penetrates into the adjacent tracheids, especially in wounded roots.

Among the lignites gathered at Kreischerville, Staten Island, on several occasions in company with Dr. Arthur Hollick of the New York Botanical Garden, the writer found some specially well preserved ones in the Drummond pit, still coated with their inner bark. These lignites showed all the features of wood structure, which are found in the living *Agathis* and *Araucaria*, and differed as a consequence markedly from the Araucarian lignites found most abundantly in the adjoining Androvette pit, from which the major part of the material of *Brachyphyllum* has been derived. Fortunately the material from the Drummond pit showed numerous healed wounds, not only in the deeper layers of the stem, but also on the surface as well. The outside of the specimens was, in fact, in some cases marked by numerous cicatrices, representing healed wounds

of considerable extent. It was consequently possible in this case to compare with the wound reactions of the living Araucarineae those of a closely allied form from the Raritan Cretaceous. Photograph 14, Plate XXVIII, which is exactly on the same scale of magnification as those of *Brachyphyllum* shown in photographs 1, 5, 6, 7, and 9, shows a transverse view of the normal wood of the species above mentioned, from the Drummond pit. The field includes part of two annual rings, and the fossil wood differs clearly from that of *Brachyphyllum*, as described in earlier paragraphs, in the presence of resinous elements similar to those found in the wood of the living Araucarineae. These can clearly be made out as dark dots scattered throughout the area of the photograph. Most of the tracheids are occupied by a substance, which is apparently of the nature of a fossil mucilage, and are obviously of somewhat larger diameter than those of *Brachyphyllum*. This fossil mucilage, if such it be, is to be compared with the similar substance, which is found in the tracheids of *Araucaria* and *Dammara*, in more or less diseased stems, as indicated above. Photograph 15, Plate XXVIII, shows the margin of a wound in the species from the Drummond pit. It presents conditions identical with those found in the case of the existing *Agathis* and *Araucaria*, as illustrated by photograph 13. There is little reason to doubt that the wood in question belongs to an extinct species, in all probability of *Araucaria* or an allied genus, since Dr. Hollick has described leafy branches referable to that genus from the adjacent, although rather higher, deposits at Cliffwood, New Jersey (The Cretaceous Clay Marl exposure of Cliffwood, N.J., Pl. 12, Figs. 3*a* and 4, Trans. New York Acad. Sci., vol. xvi, 1896–7), and since remains of *Araucaria* are in general not uncommon in the Cretaceous beds of the Eastern United States. It will be well to defer the consideration of the significance of these facts until the wound reactions of other species of *Brachyphyllum* have been described.

In the spring of 1905, at the instigation of the writer, Mr. S. A. Starrat, a student in the Geological Department of this University, during the spring season in the field, collected a large quantity of lignites from the well-known Cretaceous deposits of Gay Head on the Island of Martha's Vineyard, Mass. Among these were some moderately well preserved specimens, which presented all the structural features of *Brachyphyllum*. Their attribution to this genus is farther justified by the often described occurrence in the same beds of cone scales, of the type referred by Heer to the genus *Dammara*. These in all probability, in view of the results obtained by Dr. Hollick and the writer, in the case of a very similar species from Kreischerville, Staten Island (*op. cit.*), do not belong to *Dammara* (*Agathis*) at all, but to a new and undescribed genus, to which has been given the name *Protodammara*. Reasons have been adduced in the article cited, for the conclusion that *Protodammara* represents the cone scales of

Brachyphyllum. Photograph 16, Plate XXVIII, shows a view of the wood of one of the specimens from Martha's Vineyard, under the same magnification as the wood of *Brachyphyllum* from Kreischerville, shown in photographs 1, 5, 6, 7, and 9. The tracheids are even smaller than in the latter species ; but there is the same absence of resiniferous elements in the wood, which is characteristic of *Brachyphyllum* in general. A marked feature of specific difference from the first described lignite, is the highly resinous character of the medullary rays, which appear as dark lines running across the field of the photomicrograph. Fortunately the specimen under consideration showed in one part a wound covered over by the layers of new growth, which are commonly found in injured woods. These folds contained rows of traumatic resin-canals. Photograph 17, Plate XXVIII, in which can be distinguished the same highly resinous rays as in the last photograph, shows a portion of one of these tangential rows of traumatic ducts. The ducts in this instance, as in the first mentioned species of *Brachyphyllum* (cf. photograph 10), contain mucilage as well as resin, the latter alone persisting in the sections, on account of the numerous solvents of resin employed in the process of embedding. In this respect they resemble the normal cortical resin-canals of the existing *Araucaria* and *Agathis.* Similar mucilaginous contents are found in the cortical canals of preserved leafy branches of *Brachyphyllum*, where they have not on the one hand been too much charred, or on the other hand become too much decayed in process of fossilization. This feature of the resin canals serves as one diagnostic character to separate Araucarineous remains from those of other groups of Conifers, and has been used by the writer, together with other characters, to distinguish the branches of *Brachyphyllum* from those belonging to the Cupressineae and Sequoiineae, of very similar habit (Hollick and Jeffrey, *op. cit.*).

Through the kindness of Professor J. B. Woodworth of the Geological Department of this University, the writer had the opportunity of investigating lignites showing the structural peculiarities of *Brachyphyllum*, from that classic Potomac locality, the Dutch Gap Canal. The specimens were not nearly as well preserved as those from Staten Island and Martha's Vineyard, but are nevertheless of very special interest on account of their much lower geological horizon. One of these lignites fortunately in addition to presenting the general ligneous characters of *Brachyphyllum*, showed very clearly the presence of two rows of traumatic resin-canals in remote annual rings. The wound to which these were in all probability related does not appear in the lignitic fragment, but there seems to be no reason to doubt that the canals in question are traumatic, in view of the similarity to those described in the case of material from Staten Island and Martha's Vineyard. Photograph 18, Plate XXVIII, illustrates at once the character of the traumatic canals and the rather bad state of preservation

of the wood, in this species. It resembles the species from Martha's Vineyard rather than that from Staten Island, in the resinous character of the rays; but differs from it in the much larger size of the traumatic canals, as may be seen by comparing this photograph with photograph 17. The canals contain the same mucilaginous secretion, remaining after the removal of the resinous contents by solvents, as is seen in the species of wood of *Brachyphyllum* from Martha's Vineyard and Staten Island. The reference of the present lignite to *Brachyphyllum* is further justified by the description on the part of Fontaine in his well-known monograph on the plants of the Potomac beds, of a number of leafy branches belonging to that genus, as well as to the closely allied or identical genus *Arthrotaxopsis*.

Conclusions.

In his classic and admirable treatment of the fossil Conifers in Zittel's Palaeontologie, Schenk separates those fossil Araucarian genera, characterized by often flattened two-ranked branches, as a distinct family under the caption Walchieae. This family is made to include not only the Mesozoic extinct Araucarineae of microphyllous habit, but also the Permian genus *Walchia*. Concerning the latter genus nothing need be said at the present time, since it is not closely related to forms like *Brachyphyllum*, and nothing is accurately known as to its nearer affinities, on account of the absence of necessary details in regard to its reproductive organs and internal structure. Excluding *Walchia* itself, the Walchieae comprise a number of extinct genera of very similar habit. The oldest of these is the Triassic *Ullmannia*, of which Count Graf zu Solms aptly remarks in his Palaeophytology, that it can scarcely be distinguished except stratigraphically from the Jurassic *Pagiophyllum*. *Pagiophyllum* likewise cannot be clearly separated from the Jurassic and Cretaceous genus *Brachyphyllum*, which is the subject of the present article. The anatomical characters of *Brachyphyllum* certainly justify the separation of the Walchieae from the living Araucarian type, represented by *Agathis* and *Araucaria*. It has been shown above that *Brachyphyllum* differs markedly both in the normal structure of its wood and in its traumatic reactions from the existing Araucarineae and allied species from the Cretaceous. In the absence of resiniferous elements among its tracheids, *Brachyphyllum* resembles the older Gymnosperms, as well as the arboreal extinct Lycopodiales and Equisetales. In this feature it also resembles the still existing but very ancient genus *Pinus*. With the living and, so far as we know, the extinct Abietineae, *Brachyphyllum* also agrees in the nature of its traumatic reactions, more closely than with the living type of the Araucarineae, for in this extinct and ancient genus resin-canals were formed, as a result of wounding, just as invariably as they are in the living *Picea* and *Abies*.

The question here arises, why the living Araucarineae and their nearest fossil allies should differ so strikingly in the structure and wound reactions of their wood from *Brachyphyllum*, and why the latter should resemble so strongly in its traumatic phenomena that very ancient coniferous order the Abietineae. In this connexion it is apposite to point out, that the differences in the nature of the wound reactions obtaining between *Brachyphyllum* and existing Araucarineae are precisely the same as those which exist between the genus *Sequoia* and the remaining cupressinoid Conifers. The author has shown, that in both living and extinct species of *Sequoia* resin-canals are commonly formed as the result of injury, while such a reaction does not take place, so far as our present knowledge goes, in other cupressinoid genera (The Comparative Anatomy and Phylogeny of the Coniferales, pt. I. The genus *Sequoia*; A fossil Sequoia from the Sierra Nevada). It is important too in this connexion to note, as the writer has done (*op. cit.*), that in the living *Sequoia gigantea*, resin-canals, *although occurring only as the result of injury in the older wood*, are found normally *in the first annual ring of branches which bear the cones male and female*, as well as *in the woody axis of the female cone*. In *S. sempervirens* resin-canals appear only as the result of injury. The condition of affairs found in the cupressineous genus *Sequoia* is paralleled in the Abietineous genera *Abies* and *Cedrus*, which resemble *Sequoia* in the normal absence of resin-canals in the older wood, for here too in *Abies magnifica* and *Cedrus Libani* resin-canals occur as a *normal feature of the woody axis of the cone* as well as the result of injury to the wood, while in most of the remaining species of these genera they occur only as the result of injury to the shoot organs. In the genera *Sequoia*, *Abies*, and *Cedrus*, as the writer has indicated in the works already cited, the normal occurrence of resin-canals in such regions of vestigial persistence as the woody axis of the female cone and the *first* annual ring of branches and roots (not, however, in the roots of *Sequoia*) is good evidence, taken with other data, which need not be mentioned here, but which are recorded in the articles cited above, that the resin-canals in question are an ancestral feature of the wood. In *Sequoia sempervirens*, *Cedrus atlantica*, and *Abies balsamea*, the resin-canals no longer occur normally, even in the reproductive axis, but appear only as the result of injury.

The very constant occurrence of resin-canals as the result of injury in the genus *Brachyphyllum*, in several species of somewhat extended geographical and stratigraphical range, apparently calls for some explanation, in view of the great constancy of ligneous characters and the considerable phylogenetic importance attached to them, by those whose familiarity with the structure of living and fossil Gymnosperms makes their opinion of value. In the case of *Brachyphyllum* we in all probability have to do with a wood in the stage of *Sequoia sempervirens* or *Abies balsamea*, for in this genus,

so far as we know, resin-canals appear in the wood of the stem only as the result of injury. If the course of reasoning adopted in the case of the Abietineae and the genus *Sequoia* is correct, it may be assumed that *Brachyphyllum* has come from ancestry, which possessed ligneous resin-canals like those present in the living *Pinus* and its nearer allies, as well as in the fossil genus *Pityoxylon* Kraus. Ward has recently described a Triassic wood, which he names *Araucarites monilifera* (Monographs of the U.S. Geolog. Survey, 48, pp. 34, 35, Pl. 3) in which moniliform flattened masses of a secretion are found in the wood. He interprets these as a fossil resin. Very much larger traumatic resin-canals than those found in *Brachyphyllum* would give rise to just such moniliform rows of 'tears' of resin. It is unfortunate that this wood has not yet been structurally determined. The abundant occurrence and large size of the resinous masses would point to a condition of resiniferous activity of the wood corresponding more to that found in *Pinus* and its allies, than to that found in the Cretaceous *Brachyphylla* described above. This more abundant secretion may indicate that the older Araucarineae were more copious in their resinous exudations than their descendants of the later Mesozoic. This question can only be settled when the Triassic woods just mentioned have been subjected to proper microscopic investigation. In any case they probably belong rather to *Ullmannia* than *Brachyphyllum*. The living Araucarian genera *Agathis* and *Araucaria* and their near relatives of the Cretaceous appear to hold the same phylogenetic position towards the genus *Brachyphyllum* (and in view of the conditions found in Ward's *Araucarites monilifera*, possibly also to the older genus *Ullmannia* as well), as the cupressinoid genera as a whole occupy towards the very ancient genus *Sequoia*. For being of much more modern origin, they have quite lost the tendency to revert to the probable ancestral condition of the wood as a result of injury, which is found in *Brachyphyllum*. Such a conclusion would need, however, to be supported by structural and experimental morphological data derived from a study of fossil and living representatives of the Araucarineae, and especially the anatomical investigation of the leaves, cone scales, and reproductive axes of these, since such organs are more apt than others to retain vestigial features. Such evidence the writer hopes to supply in future articles.

In a recent memoir devoted to the Abietineae (*op. cit.*) the present writer has adduced arguments from the structure of the male and female gametophytes and from the structure and reactions of the sporophytes, for the conclusion that the Abietineae are a very ancient order of the Coniferales. This view is fortified by authentic data as to the ancient geological occurrence of cones referable to *Pinus* and *Pinites* (from the Jurassic onwards) and more especially of woods referable to the genus *Pityoxylon* (from the Carboniferous and Permian onwards). To this evidence is added that of sufficiently numerous impressions of leaves, branches, &c. (from the

Permian onwards). There is accordingly nothing inherently improbable in the derivation of the Araucarineae from an Abietineous stock. The modern representatives of the Araucarineae, however, occupy a peculiarly isolated position among the Coniferales, which has not been made less marked by the recent investigations of Penhallow on their anatomy and the very interesting results of Thomson, in regard to the growth of the pollen-tube through the substance of the ovule-bearing scales, unlike that found in any other Conifer, as well as by the discoveries of Thomson and Lopriore of numerous nuclei in the pollen-tubes of *Agathis* and *Araucaria*. The latter feature is, however, not without parallel in other Coniferous genera, since a similar phenomenon has recently been described by Juel in *Cupressus* and indicated by Coker in *Podocarpus*. It is consequently of importance to observe that the ancient Araucarian genus *Brachyphyllum* shows indications of affinity with the venerable family of the Abietineae both in ligneous structure and traumatic reactions. The wide gulf which separates the existing Araucarineae from other Coniferales, particularly from the Abietineae, is to some extent bridged over by this interesting extinct Araucarian. That this statement is not less supported by a consideration of the general normal anatomy of *Brachyphyllum*, than by experimental evidence derived from the study of traumatic phenomena, the writer hopes to show in a subsequent contribution.

Summary.

1. In three distinct species of Cretaceous Araucarian lignites, referred to the genus *Brachyphyllum*, on the basis of the study of leafy branches with structure preserved, traumatic resin-canals have been found similar to those which occur as a result of injury in the Abietineae and in the genus *Sequoia*.

2. Since these lignites have considerable stratigraphic and geographical range, it may be safely inferred that the formation of traumatic resin-canals was a constant feature of *Brachyphyllum*, and distinguishes that genus clearly from the modern Araucarineae and their relatives of the Cretaceous, which do not form traumatic resin-canals under any circumstances.

3. The traumatic reactions of the ancient and extinct Araucarian genus *Brachyphyllum* constitute one line of evidence to unite phylogenetically the Araucarineous stock with that of the Abietineae, which we now know to have been a very ancient order of the Coniferales.

The writer wishes to offer his sincere thanks to the Director of the Botanic Gardens of Buitenzorg, Java, the Director of the Botanic Garden of Sydney, N.S.W., the Director of the Botanic Garden of Harvard University, Dr. L. Cockayne, Christchurch, New Zealand, Dr. Arthur Hollick, of the New York Botanic Garden, and to Professor J. B. Woodworth, of the Geological Department of Harvard University, for numerous kindnesses in the securing of material.

DESCRIPTION OF PLATES XXVII AND XXVIII.

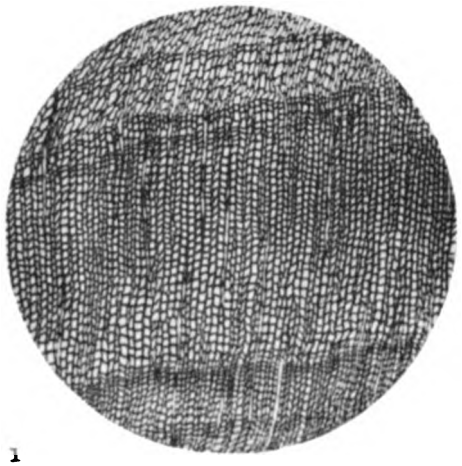
(Illustrating Professor Jeffrey's paper on *Brachyphyllum.*)

PLATE XXVII.

Photograph 1. Wood of *Brachyphyllum macrocarpum*, Staten Island. × 40.
Photograph 2. Longitudinal radial view of the same. × 200.
Photograph 3. Transverse section of wound of same. × 12.
Photograph 4. The same at another plane of section. × 12.
Photograph 5. Right margin of wound in photograph 4. × 40.
Photograph 6. The same farther to the right. × 40.
Photograph 7. Transverse section of the same wood at another plane. × 40.
Photograph 8. Part of a similar section to show resin-canal. × 200.
Photograph 9. Longitudinal section of the same lignite. × 40.
Photograph 10. Transverse section of another specimen. × 40.
Photograph 11. Centre of a wounded branch of *Brachyphyllum macrocarpum*. × 40.
Photograph 12. Part of the same highly magnified to show the traumatic resin-canals. × 200.

PLATE XXVIII.

Photograph 13. Margin of a wound in *Agathis alba*. × 40.
Photograph 14. Wood of a Cretaceous plant allied to *Araucaria*. × 40.
Photograph 15. Margin of a wound from the same material as 14. × 40.
Photograph 16. Wood of a *Brachyphyllum* from Martha's Vineyard. × 40.
Photograph 17. Traumatic resin-canals from the same. × 40.
Photograph 18. Traumatic resin-canals from a *Brachyphyllum* from the Dutch Gap Canal, Potomac beds. × 40.



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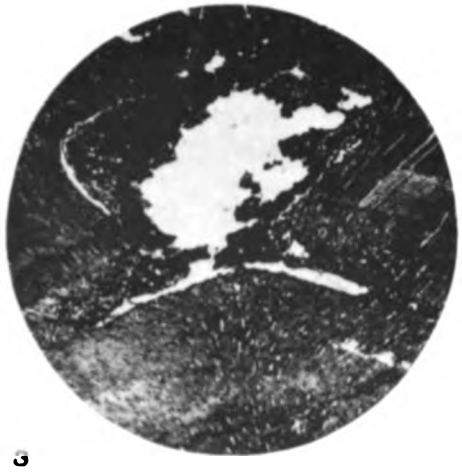

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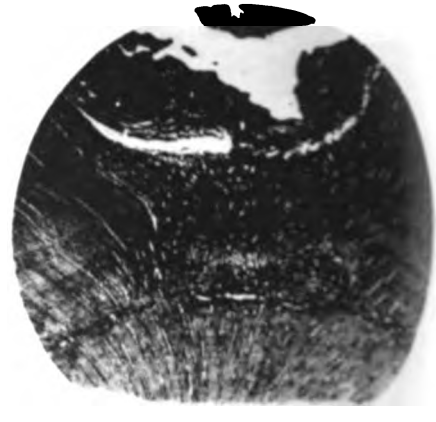

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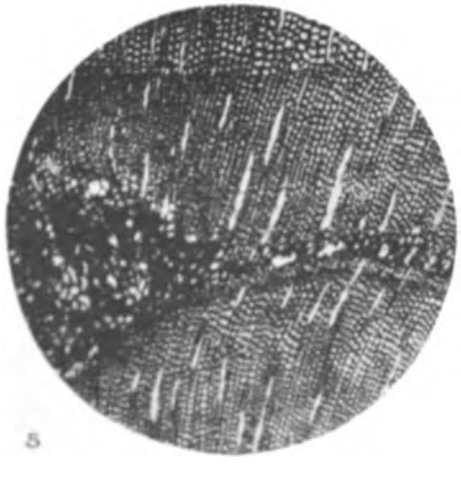

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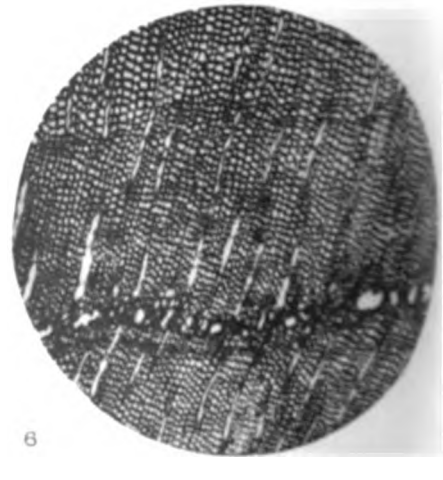

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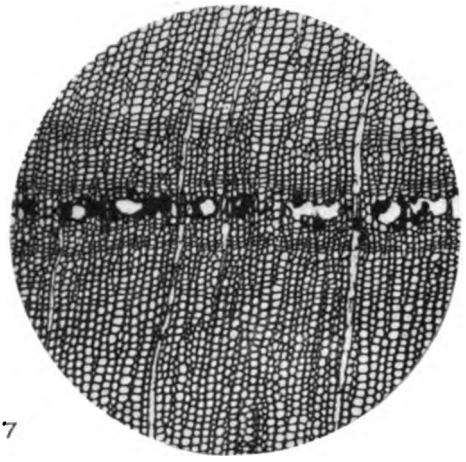

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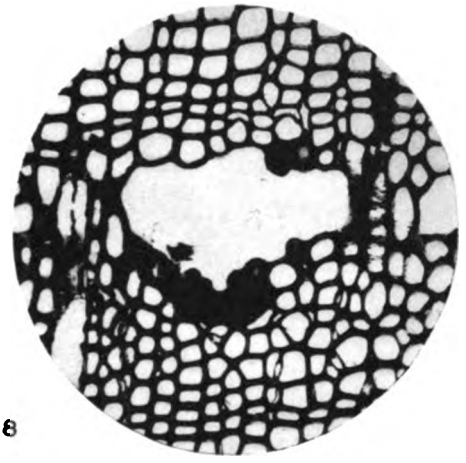

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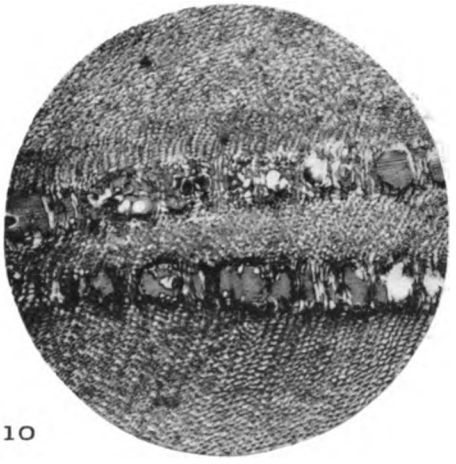

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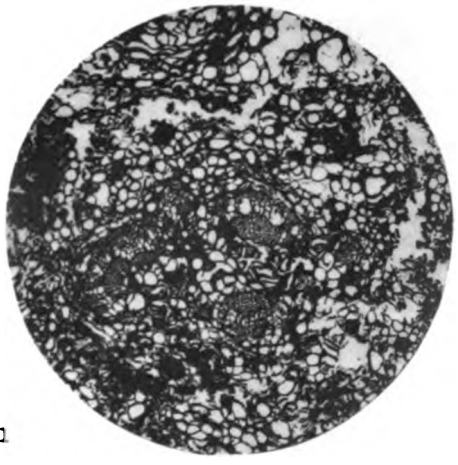

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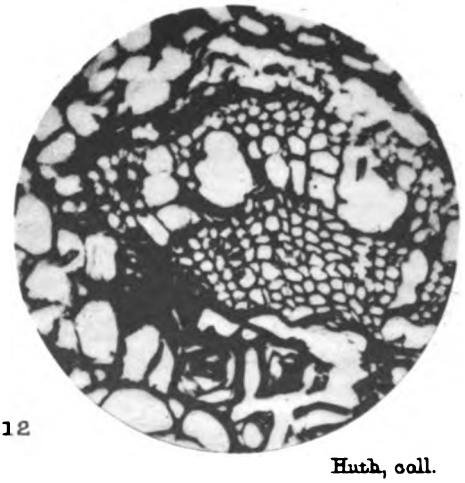

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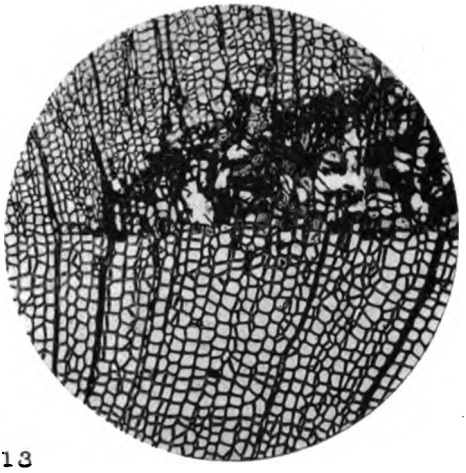

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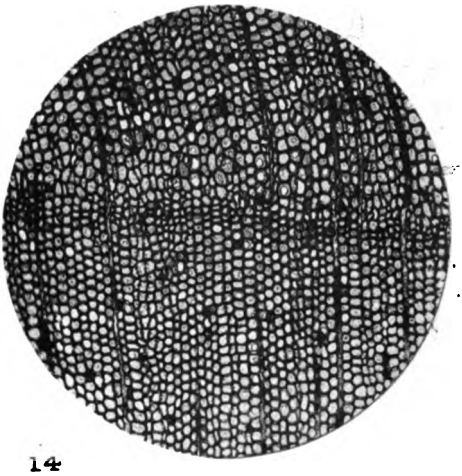

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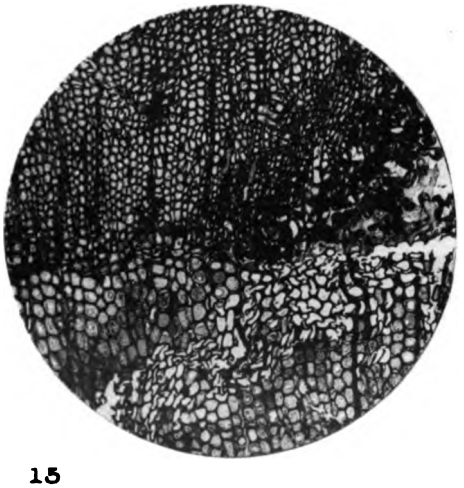

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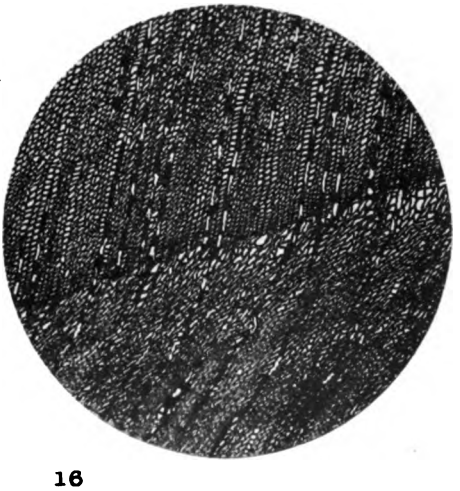

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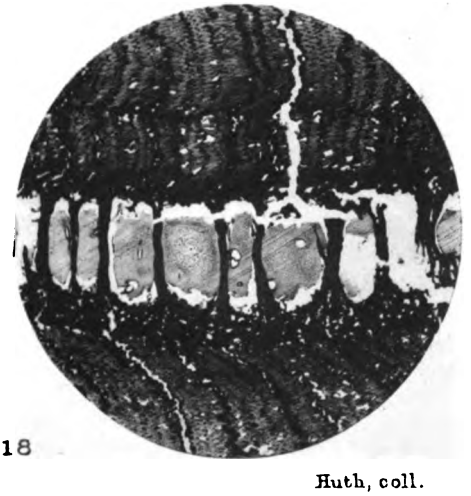

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The Morphology and Seedling Structure of the Geophilous Species of Peperomia, together with some Views on the Origin of Monocotyledons[1].

BY

ARTHUR W. HILL, M.A.

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With Plates XXIX and XXX and three Diagrams in the Text.

AMONGST the numerous species of the genus *Peperomia* which are found in South and Central America, a few peculiar species have been discovered which are more or less geophilous in habit, having either an underground corm or tuber, or a tuberous rhizome. The possession of more or less peltate leaves also appears to be correlated with the tuberous habit. De Candolle[2] has grouped these species together by means of this character, and they form the first subdivision in his arrangement of the genus. Dahlstedt[3], in his recent monograph of the South and Central American Piperaceae, follows on the lines of Miquel's arrangement, and places these species in the section *Eutildenia* of the subgenus *Tildenia*, Miq.[4] The first group of this section, which includes eleven species, is distinguished as having 'tuber hypogaeum rhizoma tuberosum,' and nearly all these species, together with some others as yet undescribed, form the subject of this paper.

In the course of my travels in the Andes of Bolivia and Peru from January to March, 1903, I found three or four different species of small bulbous Peperomias growing, either on the exposed hillsides or in clefts of the rocks, at about 13,000 feet above sea-level, and it was partly owing to the difficulty of determining the species, and partly to the discovery of

[1] Read in part before the Botanical Section of the York Meeting of the British Association, August, 1906.

[2] De Candolle, Prod. XVI, i, p. 393.

[3] Dahlstedt, Stud. über Süd- und Cent.-Amer., Peperomien, Kgl. Svenska Vet. Akad. Handlingar, Bd. xxxiii, No. 2, Stockholm, 1900.

[4] Miquel, Syst. Pip., p. 69.

[Annals of Botany, Vol. XX. No. LXXX. October, 1906.]

a large number of seedlings in the moss surrounding some of the plants, that I was led to investigate all the bulbous and tuberous specimens of this genus preserved in our herbaria, in addition to those in my own collection. These peculiar geophilous forms, which are often less than an inch in height, occur in South America, in the Andes of Peru, Bolivia, and Northern Argentina, and in Central America, in the mountains from Guatemala to Mexico.

The South American specimens resemble minute *Cyclamen* plants in their habit of growth to a very close degree. In all the known species the underground portion is a corm or tuber, which is more or less spherical, but becoming ovoid, or rather irregular in shape, in old plants. There appear to be two types of corm or tuber exhibited by the South American species. In the one case the roots are borne in a median basal tuft on the under side of the corm, in the position of the primary root, and to this type belong *P. parvifolia*, C. DC. (Fig. 27, Pl. XXIX), *P. verruculosa*, Dahlst., &c.; whilst in the other case, of which *P. peruviana*, (Miq.) Dahlst.[1] (Figs. 1 and 2, Pl. XXIX), *P. macrorhiza*, and *P. umbilicata*, R. and P. [1], &c., appear to be typical, the median primary root is supplanted by lateral adventitious roots arising from the sides of the tuber. The leaves, though they differ in shape and texture, &c., are always radical, and spring from the upper surface around the growing point or shoot-apex, and there is no trace of an erect stem; in some old bulbs two or three groups of leaves may be seen on the upper surface of the corm, owing to the branching of the originally single stem-apex.

The Central American specimens are distinct from those of South America as regards their general vegetative habit, and they fall into two well-marked groups, in accordance with the morphological character of their underground tuberous portions. In one group—to which *P. umbilicata*, H. B. and K., *P. gracillima*, Wats., and *P. pedicellata*, Dahlst. (Fig. 32, Pl. XXX), &c., belong—there is a small smooth, more or less spherical underground tuber, and the roots arise from a spot on the upper surface to one side of the shoot-apex [2].

In the other group—which includes *P. mexicana*, Miq. (Fig. 42, Pl. XXX), *P. macrandra* C. DC. (Fig. 46), &c.—there is an underground tuberous rhizome, which may be either short and stunted or branched and

[1] There is some difficulty with regard to Gaudichaud's specimens collected in Peru in about 1834, which have the number 150 and are referred both to *P. peruviana* and *P. umbilicata* (vide Dahlst., l. c., pp. 31 and 33). M. de Candolle has been good enough to send me a small specimen of Gaud. No. 150 from his herbarium. The roots were found to arise from the top of the tuber after the manner of the Mexican species (cf. *P. pedicellata*, Fig. 32, Pl. XXX), and in this particular it is quite distinct from either *P. peruviana*, *P. umbilicata*, R. and P., or any other South American species. It thus appears that Gaud. No. 150 is either a new species for South America, affording a link with the Mexican forms, or that some Mexican specimens have been accidentally placed on the Herbarium sheets with Gaudichaud's original specimens from Peru.

[2] Cf. footnote on Gaud. No. 150.

creeping; in both cases adventitious roots are borne on the rhizome[1]. The arrangement of the leaves agrees with that described for the South American species. Perhaps the most interesting point brought to light by a study of these plants is the structure of their seedlings, together with the mode of germination and development of the mature plant. These features will be described in detail under the headings of the separate species; but, for the sake of clearness, it may be stated here that in all the various species whose seedlings have been found, the structure is modelled on the same plan[2]. The seedlings have all the external characteristics of those of Monocotyledons, for the seed is hypogeal and contains an absorbent organ, whilst a small green leaf protrudes above the soil (Fig. 7, Pl. XXIX). On examination, however, it is found that both cotyledons are present, but that they have become modified to perform different functions, for one remains permanently within the seed and serves to absorb the reserve materials from the perisperm, whilst the other is drawn out of the seed and serves as an assimilating organ (cf. Fig. 8, Pl. XXIX, and Text-figs. 3–5, p. 402)[3].

As has been mentioned above, the geophilous species from South and Central America appear to be distinct from one another, and after a careful examination of all the available material at Kew and at the British Museum, it seems highly probable that these two widely separated districts are now quite distinct regions, at any rate as far as this particular group of plants is concerned, and that they have no species in common[4]. Thus, so far as our knowledge goes at present, there appears to be a large tract of country, extending from Peru to Guatemala[5], from which we have no record of any geophilous species with a pseudo-monocotyledonous method of seed-germination; whether forms like *P. Sprucei*, C. DC.[6], from the borders of Peru and Ecuador, which appear to have a more or less tuberous rhizome and radical leaves, should be included is uncertain; but although no seedlings have been found, the locality[7] for the species suggests that it is probably not a member of this pseudo-monocotyledonous group.

A great deal of confusion about the various bulbous species and their habits exists in the literature of the subject, and even the recent monograph by Dahlstedt has failed to clear up the matter satisfactorily. According to the different authorities[8], *P. umbilicata*, R. and P.[9], is recorded

[1] In *P. ovato-peltata*, C. DC., from Costa Rica, the roots emerge from the upper surface of the tubers.

[2] In addition to the material collected in Peru, I have had the good fortune to find seedlings and young plants in various stages of development in the dry mud adhering to the roots of several Mexican specimens in the Herbaria of Kew and of the British Museum.

[3] Vide Hill, A. W., Proc. Camb. Phil. Soc., xiii, p. 20, 1905.

[4] Vide footnote, p. 2, Gaudichaud, No. 150.

[5] A distance of about 2,000 miles by land and of about 1,500 miles in a direct line.

[6] Seeman's Journ. Bot., 1866, iv, p. 133; Prod., XVI, i, p. 394; Dahlst., l. c., p. 41.

[7] Tarapoto, on a tributary of the Huallaga, NW. Peru, alt. 1,170 ft.

[8] Miquel, Syst. Pip., p. 70; C. DC., Prodromus, XVI, i, p. 393; Dahlst., l. c., p. 31.

[9] The species was founded by Ruiz and Pavon (vide Fl. Peru, p. 30) on a Peruvian specimen.

not only from Peru and Bolivia, but also from Guatemala and from Mexico. An examination of the original description and figures of the *P. umbilicata* of Ruiz and Pavon [1] shows that their specimen bore roots from the sides of the tuber; but in the figure of *P. umbilicata* given in Humboldt and Bonpland [2] the tuber is globose, and the roots all spring from its upper surface, almost at the same spot, which is to one side of the point of insertion of the leaves.

From these figures it is clear that *P. umbilicata*, R. and P., and *P. umbilicata*, H. B. and K., are distinct species, and the present confusion of the two is due to the fact that these differences in the tuber have not been recognized by Miquel, De Candolle, and others, owing perhaps to the general external similarity of these two species. There are several specimens from Mexico in the Herbarium at Kew which agree with *P. umbilicata*, H. B. and K., and *P. gracillima*, Wats., is undoubtedly a very close ally of these forms [3].

In addition to these, there is yet another species, collected by Pringle [4] in Mexico, and formerly considered to be a glabrous form of *P. Müller*i, C. DC. As in the other cases mentioned, seedlings have been found which show the same monocotyledonous habit, but the mature plant possesses a well-defined creeping and somewhat tuberous rhizome. This plant, which has been named *P. macrandra*, C. DC.[5], seems from the structure of its fruits and the character of its rhizome to be nearly related to *P. mexicana*, and is a totally distinct plant from the true *P. Müller*i [6].

Fruit and Seed Structure.

Dahlstedt in his monograph has laid particular stress on the fruits as affording reliable specific characters, and, as far as the geophilous species are concerned, I have found that they furnish very valuable evidence, especially when seen in longitudinal section, as to the probable relationship of the different species (Figs. 3, 8, 29, Pl. XXIX; Figs. 31 and 41, Pl. XXX).

Moreover, owing to the retention of the fruit by the germinated seedling, there is no difficulty in the identification of seedlings which may be collected in the field. The details of the fruit-structure will be given when the several species are described, but with regard to the seeds it will be useful to make a few general remarks in this place. Owing to the similarity of the seeds of the species under consideration with those of *P. pellucida*.

[1] Ruiz and Pavon, Fl. Peru, i, p. 30, Tab. 45, Fig. *b*.

[2] H. B. and K., Nov. Gen. et Spec., i, p. 59, Tab. xv, Fig. 1.

[3] The specimen from Guatemala included under *P. umbilicata*, R. and P., No. 1430, J. D. Smith (vide Dahlst., l. c., p. 31), is a new and distinct species.

[4] Pringle, No. 4654 in Herb. Kew and Herb. Brit. Mus., determined as *P. Müller*i (glabrous form) by C. de Candolle.

[5] C. de Candolle, Ann. du Conserv. et Jard. Bot. Genève, 1898, p. 276.

[6] C. DC., Linnaea, xxxvii, p. 366.

Kunth, which have been described by Johnson [1], it will not be necessary to do more than point out a few of the most important features of their internal structure. As in that species, the single integument appears to be composed of two cell-layers, which ripen to form a brown investment to the seed ; within the testa the bulk of the seed is composed of the perisperm, the embryo with its endosperm occupying only a very small space at the apex of the seed just under the micropyle (Figs. 3, 8, 29, Pl. XXIX ; and Fig. 31, Pl. XXX). The cells of the perisperm are closely packed with starch, which is entirely absent from the endosperm-tissue in the dormant seed. The outermost layer of the perisperm differs somewhat in the structure of its cell-walls and in the nature of the cell-contents from the rest of this tissue ; with Methylene Blue and Eosin the walls of this layer take on a deeper coloration than those of the inner cells, but with Water Blue they remain unstained, while the walls of the mass of the perisperm stain violet blue. The cell-contents also differ in that some other small bodies besides starch are present, which stain violet with Water Blue and orange yellow with Iodine, and one is reminded in general appearance of the aleurone layer in the endosperm of grasses. Besides starch, some other highly refractive bodies, whose nature is as yet undetermined, are found in the general perisperm-cells.[2] The structure of the embryo and endosperm, their relations to one another in the dormant seed, and the earliest stages in the germination of the embryo in these geophilous species, appear to agree in all essentials with the account given for *P. pellucida* (vide Text-figs. 1 and 2, p. 402).

The interesting problem of the relation of the endosperm to the perisperm, in this and other genera with a similar seed structure, is discussed by Johnson [3]. He produces a considerable amount of evidence to show that the food-material stored in the perisperm can only be utilized by the embryo with the aid of the intervening thin sac of endosperm-tissue, and some further support is lent to this view by a somewhat inconclusive paper by Lewis [4] on the development of the seed of *Phytolacca decandra*. Sections of the seeds of my own species in an advanced stage of germination show a definite deeply staining layer of compressed and disorganized cells attached to the perisperm and surrounding the cotyledon (Fig. 16, Pl. XXIX; cf. also Text-figs. 3–5, p. 402). This layer appears to be the remains of the endosperm, through which the reserve materials must have passed from the perisperm to the developing embryo. The sheathing endosperm was also very clearly seen in a young seedling of *P. umbilicata*, H. B. and K.[5] (Fig. 30, Pl. XXIX).

[1] Johnson, Bot. Gaz., vol. xxx, p. 7; ib., vol. xxxiv, p. 329; Campbell, Ann. Bot., vol. xv, p. 111.

[2] Cf. Johnson, l. c., p. 6.

[3] Johnson, xxxiv, pp. 334–5.

[4] Lewis, Johns Hopkins Univ. Circ., New Ser., 1905, No. 5, p. 34, with figures.

[5] Vide p. 398.

The exact relation of the endosperm to the perisperm has not as yet been determined, but it seems probable that its function may be to produce the ferment (? diastase) by means of which the reserves in the perisperm are presented in a soluble and easily absorbed form to the developing embryo [1].

It is of interest to notice that the relations of the endosperm both to the perisperm and to the embryo are of the same nature in the case of the normal dicotyledonous embryo of *P. pellucida*,—where both the cotyledons become green,—as they are in the case of the pseudo-monocotyledonous embryo of these geophilous Peperomias, where one of the cotyledons never leaves the seed, and is purely an absorptive organ (cf. Text-figs. 1–5, p. 402). This fact, coupled with others, to be mentioned later [2], such as the occurrence of stomata, tends to show that this unique method of germination is of fairly recent origin in the genus.

South American Species.

The fruits of the geophilous species from South America present various well-marked external differences as to their general shape, whether sessile or stalked, the length of the stigma, and the appearance of the pericarp, rough or smooth, &c.; but when examined in section they appear to fall into two groups, which are distinguished from one another by the character of the pericarp—whether it forms a broad or narrow belt of cells—and by the nature of the glands, which may consist of a group of cells at the bottom of a pit (Figs. 18–20, 29, Pl. XXIX), or of only a single cell in a slight depression (Figs. 3 and 4, Pl. XXIX; Figs. 31 and 41, Pl. XXX).

It will be more convenient to describe the fruits in detail and the method of germination of the seeds under the heads of their respective species.

P. peruviana.

P. peruviana [3], (Miq.) Dahlst. The fruit [4] is about 1·3 mm. in length by ·5 mm. in breadth, containing a seed about ·6 mm. by ·47 mm. (Fig. 3, Pl. XXIX). The fruit-wall, as seen in section, is composed of 3–4 layers of cells, the two or three inner ones being easily crushed and somewhat tangentially elongated; all the cells of the pericarp apparently contain chlorophyll. The fruit is bounded externally by a layer of curved and tangentially elongated cells with fairly thick brown walls. Interspersed amongst these at more or less regular intervals are smaller isodiametric cells, slightly sunk below the surface in broad shallow pits (Figs. 3 and 4, Pl. XXIX). These latter cells have unthickened walls and peculiar

[1] Cf. Johnson, l. c., p. 333.

[2] Vide pp. 403 and 409.

[3] This species, which I collected on the damp hillsides above Guaqui at the south end of Lake Titicaca in Bolivia (alt. 13,000 ft.), has been kindly determined for me by Dr. Dahlstedt, to whom I sent my specimens.

[4] Vide Dahlst., l. c., Fig. 9, Pl. I.

refringent contents; they are of the nature of gland-cells (vide p. 405), and remind one of the similar glands on the upper surface of the leaves of these plants or of the glands in *Limoniastrum monopetalum* [1].

They appear to be of the nature of hydathodes [2], and no doubt in this species, which was found growing in damp and shady places, they serve for the excretion of the excess of water. The apex of the fruit, or rather the style, is seen in longitudinal section to be mainly composed of a group of reticulately thickened cells.

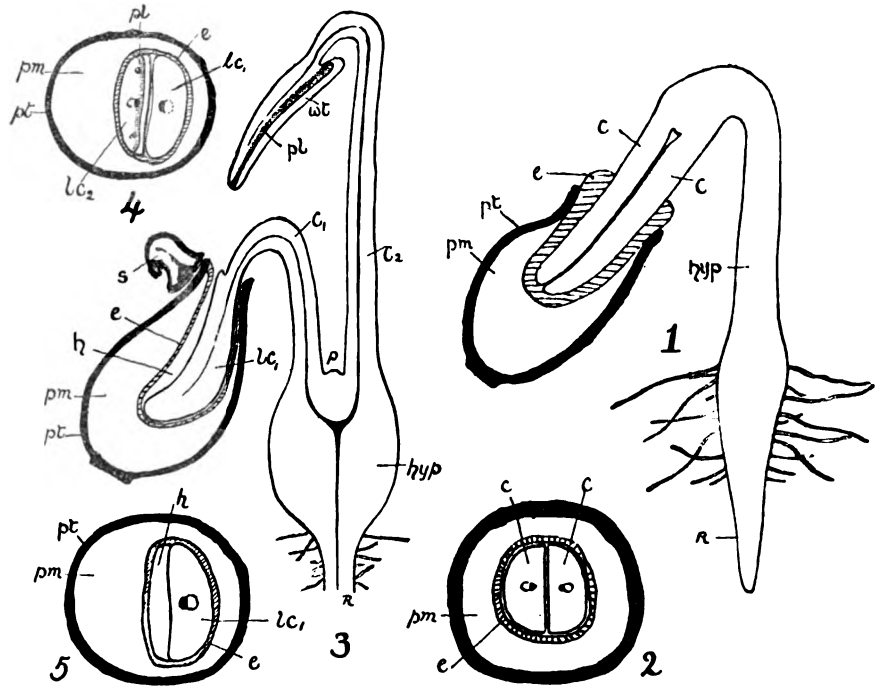
Germination.

P. peruviana. The earliest stages in the germination of the seeds of this species have not been discovered, but some of the material is sufficiently young to suggest that the commencement of germination agrees with that of *P. pellucida*, described by Johnson [3]. The stigmatic portion of the carpel is pushed aside by the outgrowing radicle, and is sometimes found adhering to the pericarp wall (Text-fig. 3, p. 402); the radicle grows vertically downwards into the soil and anchors itself by root-hairs. The two cotyledons lying face to face within the seed, surrounded by the endosperm, absorb the food material and pass it outwards along their petioles to be redeposited in a small hypocotyledonary swelling, which very early makes its appearance just below the point of union of the two cotyledon stalks with the axis (Fig. 5, Pl. XXIX; Text-figs. 1–4, p. 402). From this point onwards the whole course of the germination differs from that of *P. pellucida*, and as far as I am aware from any other dicotyledonous plant. The hypocotyl remains quite short and becomes bulbous, and starch is deposited in its cells (contrast Johnson, Figs. 37 and 39, also Text-figs. 1 and 3, p. 402, 1–4, p. 420). At the same time the petiole of one of the cotyledons, which is also the larger, elongates whilst the lamina is still within the seed, so that it becomes sharply bent after the manner of the seed-leaf of the Onion; this growth continues until the whole of the leaf is pulled out of the seed, and on emerging from the soil it becomes erect and expands into a small green and slightly peltate lamina (Figs. 5–8 and 13, Pl. XXIX; Text-fig. 3, p. 402). The lamina of the smaller cotyledon, however, never leaves the seed, and its petiole remains quite short and slender.

Thus we have here a very beautiful example of the differentiation of labour between the two cotyledons, for whilst one serves entirely as an absorbent organ and is hypogeal, the other is epigeal, and though no doubt the latter is able to absorb some reserve material when within the seed, its main function is that of assimilation (cf. Text-fig. 4, p. 402). In these particular seedlings the laminae of the two cotyledons are somewhat

[1] Wilson, Ann. Bot., iv, p. 243.
[2] Haberlandt, Phys. Pflanz.-Anat., ed. ii, p. 417.
[3] Johnson, Bot. Gaz., xxxiv, p. 331; cf. Figs. 34, 36, 37.

similar in general outline, being more or less oblong, but the absorbent cotyledon has only a single median vascular bundle, whilst the other has in



Text-figs. of *Peperomia* Seedlings.

pt = wall of the seed; *s* = the remains of the style and micropyle pushed to one side; *pm* = perisperm; *e* = endosperm; *c* = cotyledons; lc_1 = lamina of absorbent, lc_2 = lamina of assimilating cotyledon; *h* = space left in the endosperm by the removal of c_2; *wt* = water-storing tissue; *pl* = palisade-tissue; *p* = plumule; *hyp* = hypocotyl; *R* = primary root.

FIGS. 1 and 2. *P. pellucida* (after Johnson).

1. A young seedling in median longitudinal section. The two cotyledons are being withdrawn from the endosperm.

2. The seed in transverse section, showing the two similar cotyledons surrounded by the endosperm. The perisperm forms the bulk of the reserve tissue of the seed.

FIGS. 3–5. *P. peruviana.*

3. A seedling in median longitudinal section, showing the seed with one slightly peltate cotyledon lying in the pouch of the endosperm. The other cotyledon (c_2) has been withdrawn from the endosperm, leaving a hollow space, and will form an assimilating organ. The palisade-tissue (*pl*) is indicated beneath the water-storing tissue (*wt*) on the upper surface of the lamina. The hypocotyl is becoming swollen to form a corm.

4. A seed in transverse section in an earlier stage of germination than Fig. 3. The laminae of both the cotyledons are still within the seed. The two laminae show dissimilar structure; that of the absorbent cotyledon, lc_1, remains undifferentiated with a single median vascular bundle, whilst the lamina of the cotyledon which will become the assimilating organ shows a trace of water-storing tissue and of the palisade-layer on its upper surface; also there are three vascular bundles.

5. A seed like that in Fig. 3 in transverse section; the assimilating cotyledon has been withdrawn, leaving a hollow space (*h*) within the endosperm; the other cotyledon (lc_1) is left in the seed as the absorbent organ (cf. Fig. 16, Pl. XXIX).

addition a lateral curved bundle on each side bending towards the median one near the apex of the lamina (Fig. 8, Pl. XXIX, and Text-fig. 4, lc_2).

In section the epigeal lamina shows water-tissue on the upper surface between the epidermis and palisade-tissue (Text-figs. 3 and 4, p. 402), and stomata and hydathodes on the lower surface.

The lamina of the hypogeal cotyledon, which is also slightly peltate (Fig. 8, Pl. XXIX; Text-fig. 3, p. 402), is seen to be about five to six cells in thickness in a transverse section; it remains, however, undifferentiated as far as its internal tissues are concerned (Fig. 16, Pl. XXIX). In one case two hydathodes were seen near the base, and in all the seedlings examined there were two or three stomata at the apex of the lamina, apparently on the lower side. The stomata in most cases had no starch in their guard-cells [1], but in two cases, where a stoma was seen near the middle of the lamina, starch-grains were present. It seems quite clear then that we have here to deal with a dicotyledonous embryo, not only on account of the evidence afforded by the majority of the species of this genus, but also from the fact that the two leaves of the young seedling are directly opposite each other and lie with their upper surfaces in contact in the seed (Fig. 13, Pl. XXIX; cf. Text-figs. 2 and 4, p. 402). Moreover their vascular bundles unite directly under the plumule at the same horizontal level to form the central stele of the hypocotyledonary bulb and radicle (Figs. 8 and 14, Pl. XXIX).

The plumule remains inactive throughout the early stages of germination just described, and is seen to consist of a small dome of undifferentiated meristematic cells (Fig. 14). The young fully developed seedling at the end of the first stage of its development thus consists of the two cotyledons, with the rudimentary plumule, a small hypocotyledonary tuber stored with starch, and the primary root (Figs. 7 and 8, Pl. XXIX).

After a time, perhaps at the commencement of the dry season, the aerial cotyledon withers, and eventually leaves a scar, and the young plant, consisting of a small bulb with its primary root, becomes dormant (Fig. 9, Pl. XXIX). The hypogeal cotyledon, however, is not cut off from the bulb, and its lamina still remains within the seed, although it may be dead and withered and all the reserves of the seed exhausted. It is quite common to find the seeds attached to the withered cotyledon of fairly large plants (Figs. 10–12, Pl. XXIX; Fig. 39, Pl. XXX). With the return of favourable conditions the plumule produces the first leaf, and until the plant has attained to some size it never apparently has more than one leaf expanded at a time (Figs. 10–12, Pl. XXIX). Some idea of the age of a little bulb may thus be gathered from the number of leaf-scars or petiole-remains which can be found at the apex of the bulb [2], though whether only one or several plumular leaves are produced in succession during this second period of activity is unknown (cf. Fig. 12, Pl. XXIX). It is also uncertain how long a period elapses before a bulb is developed which is capable of flowering. The lamina

[1] Cf. *P. pedicellata*, p. 409.

[2] These small bulbs are spherical, and measure about 1·5 to 2 mm. in diameter.

of the first and succeeding plumular leaves differs from that of the aerial cotyledon in being circular in outline and truly peltate, with the insertion of the petiole in the middle of the lamina. It is a somewhat delicate structure, without prominent veins, which becomes thin and membranous when dried (Figs. 10–12, Pl. XXIX). In a transverse section there is seen to be a layer of clear, colourless, and sharply defined water-storing tissue on both the upper and lower sides of the lamina, some three cells in thickness, between which comes the narrow belt of assimilating tissue. This latter consists of three rows of cells, the upper one being the palisade-layer of short cells, with two layers of mesophyll cells below, and all containing chlorophyll. Stomata and hydathodes occur in the lower epidermis, and the latter occur sparsely on the upper epidermis, they take the form of a protruding glandular cell with a basal cell below ; they are also found on the petioles.

A transverse section of one of these young bulbs shows that the brown colour is due to the old and dead outermost layer of cells, which have been cut off by a layer of hypodermal cork, some four to six cells in breadth. The outermost layer of the bulb is apparently a true epidermis, since the bulb seems to be formed from the hypocotyl. The radicle of the embryo may persist for some time, growing in length and producing lateral branches, though as a rule, shortly after the development of the first plumular leaf, new roots, which ramify extensively, arise from the sides of the little bulb, and soon replace the primary root (Figs. 11 and 15, Pl. XXIX). The young bulb, at first white externally, soon becomes of a bright brown colour, and at this stage is covered, like the roots, with fairly long epidermal hairs (Fig. 10, Pl. XXIX).

Owing to the absence of certain stages in the development of the bulbs it is not clear how the 'hairs' arise, for they do not occur on the hypocotyl of the seedling, though root-hairs are found in abundance on the radicle.

The old bulbs or corms of this species (*P. peruviana*) are about 8 mm. in breadth by 10–12 mm. in length ; they are more or less spherical, but with age often become somewhat irregular in shape, and the roots, which are adventitious in origin, are scattered over the base and sides (Figs. 1 and 2). When the plants were collected in February, they were in full vigour, with a crown of leaves and inflorescences, and the oldest fruits were already ripe: it is possible that the germinating seeds which were found may have been produced this same season [1].

P. PARVIFOLIA.

P. parvifolia, C. DC. The fruit in this species differs considerably from that described above ; it is about 1·4 mm. long by 1 mm. broad, and contains a seed measuring about ·8–9 mm. by ·65 mm. (Fig. 18, Pl. XXIX).

[1] Cf. Johnson, l. c., vol. xxxiv, p. 330.

Externally the fruit appears pitted or corrugated, and has a short dome-like stigmatic cap [1], which is in great contrast to the nearly smooth fruit of *P. peruviana* with its relatively long stigma (cf. Fig. 3, Pl. XXIX) [2]. In section the fruit-wall is composed of four or five internal layers of parenchymatous cells more or less alike, though the cells of the layer next the integument tend to be tangentially elongated. The outermost or epidermal layer consists of thick-walled square or oblong cells interrupted by frequent pits, at the base of which are the gland-cells (Figs. 18–20)—groups of four cells in the tissue of the pericarp, with peculiar contents, some of which stain blue with Water Blue and appear to be of a mucilaginous nature, whilst others remain unstained and are highly refractive. The stigmatic knob is made up of a group of reticulately thickened sclerous cells. I was unfortunate in not securing any seedling stages of this species, and the ripe fruits which were collected in Bolivia would not germinate on my return home. One germinated seed, however, was discovered in my material which still enclosed the lamina of the absorbent cotyledon. The petiole of this cotyledon, which was broken off from the rest of the seedling, is much longer and stouter than is the case in *P. peruviana* (Fig. 21, Pl. XXIX).

On dissecting away the seed, the lamina of the absorbent cotyledon was found to be obovoid or club-shaped, about ·45 mm. in length by ·35 mm. in breadth, having a circular outline in transverse section. There were apparently no stomata, though this point is somewhat uncertain. The more highly specialized character of the absorbent organ in this species is of considerable interest, for the adult plant is of a much more xerophytic type than *P. peruviana*, and it seems probable that the lamina of the aerial cotyledon is withdrawn in a rudimentary condition from the seed at an early stage in the germination, and thus gives room for the development of the hypogeal cotyledon to join the aroid-like absorbent organ (vide Text-figs. 5 and 6, p. 420), which then completely fills the cavity of the endosperm (cf. Text-figs. 3 and 4, p. 420).

Of bulbs with the first, second, or third, &c., plumular leaves, several were collected, and from the nature and position of the leaf-scars there can be no doubt that a very similar course of development obtains to that already described (Figs. 23–25). The young bulbs are readily recognized by their size and their whiteness, and by the fact that the roots, which are long and much branched, are produced only from the base (Fig. 23). In a transverse section the epidermis of the bulb is seen to be protected by a thin cuticle, which stains light yellow with Iodine, but there is no formation of cork. The cortical cells, as in *P. peruviana*, are filled with starch, but whilst in that species the starch-grains are more or less rounded and small, they are here considerably larger and ovoid. The plant is a much more pronounced xerophyte than *P. peruviana* (Fig. 27), and this is very well seen

[1] Cf. Dahlst., l. c., Pl. I, Fig. 7.

[2] Dahlst., l. c., Pl. I, Fig. 9.

in the leaves, whose small ovate, orbicular laminae are rather stout and fleshy and usually slightly concave. In a transverse section of a lamina of a mature leaf there is seen to be a narrow layer of water-storing tissue on the upper surface, consisting of the epidermis and a single row of hypodermal cells, and below this is a double palisade-layer of fairly long cells; the rest of the leaf is composed of spongy mesophyll, the lowest layers of which contain no chlorophyll. Hydathodes, consisting of a protruding gland-cell with a basal cell, are sunk in deep pits, and are distributed chiefly over the lower surface of the lamina, though they occur on the petioles and inflorescence-stalks as well.

The petioles and inflorescence-stalks are short, stiff, and erect; the latter are few flowered and are not much longer than the leaves (Figs. 26 and 27, Pl. XXIX). In old plants the bulbs are generally spherical, about 10 mm. long by 12 mm. across, though in some cases they reach a length of 18 mm. (Fig. 28); in general structure they are typical corms with a single median basal tuft of roots.

This species was found in an exposed position on little damp ledges on a hillside above Copacabana, at the southern end of Lake Titicaca, some 13,500 feet above sea-level, which no doubt accounts for its pronounced xerophytic characters.

P. VERRUCULOSA SP. NOV., Dahlst., AND OTHER SPECIES.

Very similar plants, at least as far as their external morphology is concerned, were collected on the exposed hillside of the hill of Sachshuaman, above Cuzco, some 12,000 feet above sea-level.

Although no seedlings were obtained, it is clear that *P. verruculosa*, Dahlst.[1], belongs to the group under discussion, and the structure of the fruit (Fig. 29, Pl. XXIX) proves it to be a new species allied to *P. parvifolia*, C. DC. The fruit is about 1·4 mm. long by 1·1 mm. broad, and contains a seed measuring about ·7 mm. by ·55 mm.

The pittings in the pericarp wall are very much deeper than in *P. parvifolia*, and the fruit has in consequence a much rougher appearance (cf. Fig. 18). In section the pericarp consists of five rows of cells; the innermost layer, bounding the testa of the seed, is formed of fairly large, clear and tangentially elongated cells, and surrounding these are two layers of small, more or less isodiametric cells. Of the two outermost layers forming the outer wall of the fruit, the external is composed of long radially elongated and often curved cells with thick walls, which are arranged in groups. Between these groups deep pits occur, and four to six cells of the internal layer form a gland at the base of each pit (Fig. 29, *g*). The

[1] This species has been determined by Dr. Dahlstedt from my material, and his description will shortly be published.

stigmatic knob is small, and is made up mainly of a large group of cells with lignified reticulate thickening. The corms agree in general structure with those of *P. parvifolia*, and the leaves are small, stout, and fleshy as in that species; but in section the band of water-storing tissue is deeper,—owing to the greater size of its cells,—and the chlorophyll tissue, with its double palisade-layer, is more restricted than in that species.

A third species, closely allied to the two preceding, was collected near the snow line in a valley (Pacechac) near Urubamba. Ripe fruits were not obtained with this specimen, but in some cases the spikes appear to have produced vegetative buds in place of flowers. The leaves, whilst agreeing externally with those of *P. parvifolia*, are found to differ somewhat when seen in section, for below the narrow two-celled upper layer of water-storing tissue there is a well-marked triple palisade-layer, and the band of spongy mesophyll on the lower surface is devoid of chlorophyll. Should seedlings ever be found of these two latter species, there is no doubt that they would be pseudo-monocotyledonous in their method of germination.

Other species from this region are *P. umbilicata*, R. and P.[1], about which there is so much confusion. From the figure of the plant[2] it appears to be similar in habit to *P. peruviana*, Dahlst., and it is possible that these two species are identical.

P. macrorhiza, Kunth[3], and *P. scutellaefolia*, R. and P.[4], are unrepresented in our British herbaria, but from the figure of the latter species it appears to be closely allied to *P. umbilicata*, and the roots spring from the sides of the relatively large tuber.

Mexican and Central American Species.

The Mexican and Central American bulbous species appear to form a group distinct from the Peruvian forms, as I have already stated[5], although there is still considerable confusion about this matter.

P. umbilicata, H. B. and K.

One of the commonest forms in our herbaria is the species which has been confused with *P. umbilicata*, R. and P.[6], but which, as I have shown, is the *P. umbilicata* of Kunth[7]. The examples of this species have all been collected in the mountains of Mexico, in the regions to the north and

[1] Mandon's No. 1122, referred to *P. umbilicata*, R. and P. (C. DC., Prod., XVI, i, p. 393; vide Dahlst., l. c., p. 31), is without doubt *P. peruviana*, as is also Pentland's specimen collected at 12,880 ft. in Herb. Kew, and described as *P. parvifolia* in Seeman's Journ. Bot., iii, 1866, p. 133. Cf. note on Gaudichaud's No. 150.

[2] Ruiz and Pavon, l. c., Tab. 45, Fig. *b*.

[3] H. B. and K., Nov. Gen. et Sp., i, p. 72.

[4] R. and P., Fl. Peruv., i, p. 29, Taf. 44 b.

[5] Vide p. 396.

[6] Cf. Dahlst., l. c., p. 31.

[7] H. B. and K., l. c., p. 59, Taf. xv, Fig. 1.

north-west of Mexico city. The ripe fruits are very similar in external appearance to those of *P. parvifolia,* C. DC., but they differ in the character of the pericarp and gland-cells and in the more pronounced stigma. They measure about 1·4 mm. in length by 1·8 mm. in breadth, and the rounded seed is about ·85 mm. by ·8 mm. (Fig. 31, Pl. XXX)[1].

The outermost layer of the fruit is composed of thick-walled elongated cells and covered with pits similar to, but rather more shallow than, those in *P. parvifolia*; an important point of difference from this species is that only a single gland-cell occurs at the base of each pit. Below this outer layer the fruit-wall is seen, in a longitudinal section, to be only about three cells in breadth. A single young seedling was found in the Herbarium at Kew which agrees exactly with the seedlings of *P. peruviana*, of the same age, already described (Fig. 30, Pl. XXX). The relationship of the endosperm to the cotyledon and perisperm was, however, so well seen in this specimen, on dissecting away the seed, that a brief description is added.

The endosperm fitted like the finger of a glove round the absorbent lamina of the young hypogeal cotyledon, and was attached to the seed-walls all round the apex of the seed, thus shutting off the perisperm from the cotyledon. On treatment with Iodine the contents of the perisperm cells become black-purple, but the endosperm tissue stains brown like the cotyledon and only shows traces of starch, which gives a pinkish purple colour.

From the somewhat club-shaped character of the absorbent cotyledon the seedling of this species seems to occupy an intermediate position between that of the seedlings of *P. peruviana* and *P. parvifolia*.

In their later stages of development, the seedlings of *P. umbilicata*, H. B. and K., differ in an important and interesting manner from those of the South American species, and most, if not all of the other species belonging to the Central American and Mexican bulbous group show the same peculiarities. As a fairly complete series of the stages of germination and the development of the young bulbous plant of a Guatemalan species (*P. pedicellata*, Dahlst.) has been found, a description of these will suffice for the whole group.

P. PEDICELLATA.

In *P. pedicellata*, Dahlst.[2], the fruits are borne on long pedicels, which are not quite equal to them in length (vide Fig. 32, Pl. XXX). The fruit, including the stigma, is about 1·15 mm. long by ·35 mm. broad, and is linear-obovate in shape, the stigma being ·35 mm. in length; the seed measures about ·7 mm. by ·3 mm. The fruit-wall is seen, in sections, to be of the same type as the pericarp in *P. peruviana*, Dahlst., having the outermost layer

[1] The figure given by Dahlstedt of the fruit of *P. umbilicata*, R. and P., Pl. I, Fig. 8, appears to have been made from a Mexican specimen.

[2] Dahlst., l. c., p. 35, Pl. I, Fig. 13; T. D. Smith, Sta. Rosa, alt. 3,000 feet, No. 3829; O. Salvin, Volcan de Fuego, 6,400 feet, Guatemala.

composed of tangentially elongated cells with single gland-cells interspersed (Fig. 41, Pl. XXX).

In the youngest seedling stages discovered, the aerial cotyledon is fully expanded; its lamina is rotund-cordate to ovate more or less acute, about 3·5 mm. long and 2·5 mm. broad, trinerved and very slightly peltate, the insertion of the petiole being almost at the base. The hypogeal cotyledon, as in the other cases, remains embedded in the seed, and the petioles of the two cotyledons spring from a small, slightly swollen hypocotyl, which is prolonged into the short primary root or radicle (Fig. 33, Pl. XXX). On dissecting away the fruit and seed the included, absorbent lamina is found to be oblong in shape, ·6 to ·7 mm. in length, obtuse and slightly concave, with a single median vascular bundle (Fig. 34). Near the middle, and apparently on the lower side of this cotyledon, a single stoma was found in one case, with starch in the guard-cells; whilst in another case three stomata were found at the apex of the cotyledon, but there was no indication of starch. These latter stomata may perhaps be of the nature of water-stomata. Slightly older seedlings show further stages in the development of the tuber; the primary root, which at first is in a straight line with the hypocotyl and plumular dome, becomes laterally displaced, owing to the growth of the tuber taking place mainly on one side. At about the same time a lateral root is given off from the base of the primary root, and this at first grows upwards, but then bending over, keeps a more or less horizontal course at about the level of the top of the tuber (Figs. 33 and 35).

The unilateral development of the tuber continues, with the result that the point of insertion of the primary root is gradually carried round until finally the root or tuft of young roots comes to spring from what is now the upper surface of the bulb (Figs. 35–38). The point of origin of the roots thus lies to one side of the shoot-apex on the physiologically upper surface of the tuber, so that these points are separated from one another by only a small intervening space, which represents one of the sides of the hypocotyl of the young seedling. The small spherical bulb or tuber is a true corm, as in the South American species, but, owing to this curious asymmetrical development, it has assumed the appearance of a root tuber, such as one finds in *Ranunculus ficaria*. When the primary root has been brought round to the upper surface of the tuber in the manner just described, it becomes replaced by numerous lateral roots, which spring from its base; these then grow out all round over the top of the bulb in the horizontal direction, and pass on either side of the shoot with its leaves. The roots are thickly covered with root-hairs and do not branch very freely, but they all spring very definitely from one spot (Figs. 38 and 39). In an old tuber an occasional root can be found arising a little away from this spot.

Longitudinal sections through young and old tubers show this peculiar unilateral development in a very striking manner. The course of the stele in the hypocotyl of the seedling is at first vertical (cf. Fig. 34, Pl. XXX); this then becomes curved, being pushed aside by the stronger development of cortical tissue on one side of the hypocotyl, until it forms a semicircular loop at the upper end of the young tuber, uniting the now contiguous points of egress of stem and root. The main mass of the tuber is situated below this stelar loop, and consists of parenchymatous tissue stored with starch; the tuber is bounded by a cuticle, but there is no development of any corky tissue (Fig. 40, Pl. XXX).

The tuber never seems to attain to any large size; the largest seen are about 5 mm. in transverse diameter by 3 mm. in height, of a yellow colour, and often have a wrinkled skin. Since we have no precise information as to the nature of the habitats of the species which possess this type of tuber, or of the particular conditions under which they grow, it may not be very profitable to speculate on the possible reasons for this peculiar adaptation. The roots running horizontally above the tuber show that their object is to be close to the surface of the soil, and this would suggest that the need of oxygen may have stimulated them to grow in this manner. This view is strengthened on recognizing the definitely apogeotropic nature of the first lateral root of the young seedling (Figs. 33 and 34).

The leaf petioles in *P. pedicellata*, Dahlst., are some 6 to 7 cm. long, and bear cordate-peltate acute laminae, some 2·5 to 3 cm. long by about 2 cm. broad (Fig. 32, Pl. XXX). Owing to the small size of the tuber, it seems probable that the plants are able to grow actively with the help of their leaves and roots during the damp season, and are not dependent on the store of nutriment in their tubers. During the dry season or on the incidence of an unfavourable time this organ may be of great value to the plant, both in preserving its life and in affording a supply of nutriment for the resumption of active growth on the recurrence of favourable conditions.

The texture of the lamina in the dry specimen is membranous and thin, like that of *P. peruviana*, and is in marked contrast to the small thick lamina of *P. parvifolia* and its allied species. This character suggests that the habitat of the species is damp and shaded, at least during the vegetative period, and the position of the roots is also suggestive of a wet situation[1].

Other Bulbous Species.

P. umbilicata, H. B. and K.[2], is a much larger and stouter plant than *P. pedicellata*, having fairly large orbicular and medianly peltate leaves, which are firm in texture and possess clearly marked veins. The tuber is

[1] It is of interest to notice that *P. peruviana*, which bears its horizontally running roots on the sides of its tubers, also grows in damp and shady places.

[2] H. B. and K., l. c., i, p. 59, Taf. xv, Fig. 1.

described by Kunth as being about the size of a pea, but in some examples with old tubers it is considerably larger.

The closely allied *P. gracillima*, Wats.[1] is very similar to the last species, only rather more slender, and as there are no ripe fruits it is not possible to be certain whether it is merely a varietal form or a true species; both plants are said to grow in damp places among rocks, and a greater or lesser degree of exposure would of course cause a considerable difference in the appearance of plants belonging to the same species. It seems probable that *P. claytonioides*, Kunth[2] from Guatemala, *P. ovato-peltata*[3], C. DC. from Costa Rica, and *P. pinulana*[4], C. DC. from Guatemala may also belong to this same group, but it is impossible to be certain of this from the literature of the subject.

Rhizomatous Forms. P. mexicana.

Turning now to the other group of the Mexican species referred to at the commencement of the paper[5], there are two or three forms with a more or less creeping rhizome whose seedlings have been found to be of the same character as those already described. The best known and most certainly defined species in this group is *P. mexicana*, Miq.[6], which has also been described and figured under the name of *P. Galeottiana* by Hooker[7]. As the character of the underground portion is not well shown in this figure a fresh illustration is given of this species (Fig. 42, Pl. XXX).

P. mexicana occurs in the Cordillera of Vera Cruz; it possesses a short tuberous rhizome bearing lateral protuberances, which give it the appearance of a compound tuber when viewed from below. Towards the stem-apex it narrows and bears a tuft of radical leaves and the roots appear to arise from this upper narrower portion. The fruit (cf. Dahlst., l. c., Fig. 12) is distinct from that of *P. pedicellata* since it is sessile and has a long style with a peltate stigmatic head (Fig. 43). The pericarp, however, is smooth as in *P. pedicellata* and there are only single gland-cells in the shallow pits. The fruit measures about ·9 mm. long, exclusive of the style—which is about ·6 mm.—by about ·3–·4 mm. broad, and it is linear-oblong in shape.

[1] Watson, Proc. Amer. Acad., xxii, p. 448, No. 585, Palmer, Jalisco, Mexico, in deep recesses of overhanging rocks.

[2] C. DC., Prod., XVI, i, p. 400; Dahlst., l. c., p. 33. M. de Candolle kindly informs me that in this species the roots emerge from the upper part of the tuber.

[3] C. DC., Seeman's Journ. Bot., iv, p. 133, 1866; ib., Prod., XVI, i, p. 324; Dahlst., l. c., p. 34.

[4] C. DC., Engl., Jahrb., x, p. 289, 'radice reniformia Tuberosa.' Hab. Pinula prope Xalapa alt. 1,800 m. This species is considered to be a variety of *P. claytonioides*.

[5] Cf. p. 396.

[6] Miq., Syst. Pip., p. 75; Nov. Act. Nat. Cur., p. 12, Taf. vi, 1846; Dahlst., l. c., p. 34, Pl. I, Fig. 12.

[7] Hooker, Icones, vol. iv, Tab. 327.

Two seedlings were found amongst the roots of the specimen at Kew, and they agree closely with those of *P. pedicellata* already described. The hypogeal cotyledon is somewhat obovate in shape, and slightly concave, whilst the aerial cotyledon is broadly oblong, acute, trinerved, and only peltate at the base. The primary root grows vertically downwards, but at its base a lateral secondary root is very soon developed which grows upwards, and then bending out horizontally continues to grow in this direction (Figs. 44 and 45).

It is unfortunate that the whole course of the development of the plant cannot be followed in this species, but it seems probable that the roots may get carried round to the upper surface as in the other Mexican species, and that the rhizome is produced by the continued growth of the stem-apex.

The leaves of the mature plant have fairly long and slender petioles. their laminae are ovate-lanceolate in outline, trinerved, and scarcely peltate; in texture they are thin and membranous when dried, and the plants evidently grow in damp and shady places (v. Fig. 42).

Another plant, which should probably be placed here, is Hartweg's specimen[1] from Aguas Calientes in North Mexico: it has a short stout tuberous rhizome with roots arising from all over the surface. The upper part is marked by closely crowded leaf-scars. The ripe fruits with their large pericarps differ considerably from those of other species, but no seedlings have as yet been found.

P. MACRANDRA, C. DC.

The only other species of this group, of which we have knowledge of the seedlings, is a well-marked species, which appears to have been confused with *P. Müller*i, C. DC.[2], but which is now known as *P. macrandra*, C. DC. The plants in question were collected by Pringle[3] in Mexico, at an elevation of 8,500 feet; they are of particular interest in having a very definite creeping rhizome, which is somewhat tuberous in character, and bears roots on the lower side (Fig. 46, Pl. XXX).

The leaves are all radical and spring from the apex of the rhizome. and the whole plant is glabrous. The petioles have broad bases, and large semicircular or reniform leaf-scars are left on the rhizome by the fallen leaves[4]. There is no overlapping of petiole bases as in *P. Müller*i, C. DC. The rhizome is about 4 mm. in diameter. The leaf lamina is broadly ovate-lanceolate, acute, peltate with five principal veins, the insertion of the

[1] Benth., Pl. Hartweg, p. 293. This plant, No. 1621, is referred to *P. monticola*, Miq., which does not appear to be a correct determination; a plant collected by Schaffner (No. 108) at San Louis Potosi seems to be identical with No. 1621 (Herb. Kew).

[2] Linnaea, xxxvii, p. 366–7; Dahlst., l. c., p. 37.

[3] Pringle, No. 4654, on the wet ledges of the Sierra de San Felipe, Oaxaca, Mexico. Herb. Kew and Herb. Brit. Mus. Labelled *P. Müller*i, C. DC., glabrous form.

[4] Since writing this paper I have paid a visit to Geneva and find that M. de Candolle has described this plant as a new species in the Ann. du Conserv. et Jard. Bot. Genève, 1898, p. 276.

petiole being below the middle, about a quarter of the length of the lamina from its lower edge. The fruit is about ·8 mm. in length, almost sessile, and the stigma is almost equal in length to the fruit (Fig. 47).

Two young seedlings were found adhering to the dry specimen, and they are of exactly the same character as those already described in this paper (Fig. 48). Unfortunately only the cotyledonary stages of the young plants were found, and no light is thrown by these on the formation and development of the rhizome, but it seems likely, on the analogy of the other species of the group, that it must be hypocotyledonary in origin. There seems to be a fairly close relationship between this species and *P. mexicana*, not only in the fruit structure, but also as regards the general external morphology.

Of other species from Mexico *P. Mülleri*, C. DC. and *P. Bourgeaui*[1], C. DC. have well developed creeping rhizomes, which are covered by the persistent petiole bases; the plants are hairy, and the cordate leaves are slightly peltate; there is, however, no evidence to show whether or no these species belong to this pseudo-monocotyledonous group.

Anatomy.

With regard to the anatomical structure of the seedlings, there is but little to be said. The only seedlings available for section cutting were those of *P. peruviana*. A transverse section near the base of the cotyledons shows a small median collateral vascular bundle in each cotyledon, that of the aerial cotyledon being the larger, and as one passes down below the point of union of the two cotyledons, in a series of sections, these two bundles are seen gradually to approach one another. The plumule is rudimentary at this stage, being represented only by a small knob of meristematic tissue; thus the only vascular bundles in the young seedling are the two cotyledonary traces. The phloem consists of a group of delicate thin walled elements, and the xylem is composed of a few small spiral vessels. The transition from stem to root appears to take place by means of the splitting of the phloem and rearrangement of the xylem; but, owing to the state of the material, it was very difficult to follow all the changes. As far as could be seen, there did not appear to be any preparatory division of the phloem of the cotyledonary traces whilst still within the petioles[2]. The root shows a simple diarch structure, with only two or three lignified elements forming the xylem-plate (Fig. 17, Pl. XXIX)[3].

[1] Linnaea, xxxvii, p. 370; Dahlst., l. c., p. 44, Fig. 16, Pl. 1. Both these species have been collected at Orizaba in Mexico. *P. Bourgeaui* is represented at Kew by Bourgeau, No. 3230, and *P. Mülleri* by Müller, No. 653, and a Guatemalan specimen, No. 3826, of J. Donnell Smith (cf. Dahlst., l. c., pp. 37 and 44). They all agree very closely together, and there seems to be little doubt that these two species are identical.

[2] Cf. Hill, T. G., Ann. Bot., xx, p. 170.

[3] Cf. Hill, T. G., l. c., Pl. X, Fig. 6.

General Considerations.

Several points of general interest and of somewhat wide bearing are suggested by the facts which have been detailed in the foregoing pages; but, in the first place, it will be best to summarize the evidence which has been obtained from the study of these geophilous Peperomias. The internal structure of the seed has been found to agree with that which obtains in normal species of the genus, and there is little doubt that the early history of the embryo follows the usual course. In its germination, however, it reveals some striking aberrations from the dicotyledonous type common to the majority of the species, for the seedling is, in appearance, monocotyledonous.

Although the embryo is dicotyledonous in structure, the monocotyledonous character of the seedling is due to the fact that the two cotyledons show a division of labour; for whereas one serves as an absorbent organ, the other is mainly, if not entirely, an assimilating organ. That we have really to deal with two cotyledons in these species seems to me to be proved by the following considerations.

In the first place, the initial pair of leaves of the young seedling are always opposite to one another (cf. Fig. 13, Pl. XXIX), having their upper surfaces in contact within the seed, and the seedlings appear to agree very closely, in the youngest stages, with the dicotyledonous embryo of *P. pellucida*. Secondly, the vascular bundles, which are similar in structure in both the petioles, fuse together below the plumule at the same horizontal level, and appear to take equal shares in the composition of the central stele of the hypocotyl and root (cf. Fig. 14, Pl. XXIX). In the third place, it must be borne in mind that these geophilous species form a very small subgroup of a large genus whose various species, with these exceptions, show, as far as we know, a perfectly normal dicotyledonous embryo; and we have every reason for supposing that the structure of the seedlings is homologous throughout the genus.

Certain features which are noticeable during germination suggest that the monocotyledonous tendency is a fairly recent acquisition in the genus, and is, moreover, directly correlated with the adoption and development of the bulbous habit[1]. Amongst such features, the sharp bend or hook exhibited by the petioles of both of the cotyledonary leaves may be mentioned (cf. Figs. 5, 6, and 13, Pl. XXIX). This no doubt is a reminiscence of the time when both cotyledons were epigeal. Now only one cotyledon becomes aerial and bears the pressure of the soil on its sharply bent petiole (Fig. 6). In a normal species such as *P. pellucida*[2], it is seen that

[1] Cf. Darwin, C., The power of movements in Plants, p. 97.

[2] Cf. Text-fig. 1, p. 402, and Text-figs. 1 and 2, p. 420, also v. Johnson, Bot. Gaz., xxxiv, Figs. 31, 37, 39, Pl. X.

the two cotyledons remain within the seed for some time absorbing the reserve materials, and are not withdrawn until the reserves are exhausted. It is interesting to notice that these aberrant forms afford a close parallel in this respect, for at first in *P. peruviana*, and perhaps in all the other species, both cotyledons serve for a short time as absorbent organs. With the withdrawal of the aerial cotyledon, a cavity is left within the endosperm, which in *P. peruviana* is never entirely obliterated by the further growth of the absorbent cotyledon; in fact the lamina of this organ retains its dorsi-ventral character within the seed, and, moreover, is seen to be slightly peltate, thus preserving the character of a foliage leaf (Fig. 16, Pl. XXIX; Text-figs. 3–5, p. 402). *P. peruviana* thus exhibits somewhat imperfect or intermediate modifications of its seedling structure from the dicotyledonous type, which suggest that such modifications have been only comparatively recently initiated in this species.

In *P. parvifolia*, however, the modification of the seedling structure seems to have proceeded still further towards the monocotyledonous ideal, for in this species the absorbent cotyledon is obovoid, or club-shaped, and has lost its dorsi-ventral character, so that apparently it fills the cavity of the endosperm (Fig. 22, Pl. XXIX, and Text-figs. 5 and 6, p. 420)[1]. The greater degree of specialization exhibited by the seedlings of this species is of considerable interest, for the adult plants of *P. parvifolia*, *P. verruculosa*, and my own undetermined specimen from Pacechac[2], are very strongly xerophytic, and form a closely related group, which must be considered to have advanced further in their adaptation to the bulbous habit than any other of the geophilous species.

The absorbent cotyledon in *P. umbilicata*, H. B. and K.[3], also appears to be more or less spherical (Fig. 30, Pl. XXIX), and it is somewhat significant to notice that this species exhibits characters more markedly xerophytic than do its allies both in the structure of its leaves and of its fruits[4].

Further traces of the once normally dicotyledonous character of the seedlings, particularly in reference to the reduction of one of the aerial cotyledons to function wholly as an absorbent organ, are afforded by the occurrence of stomata and hydathodes[5] on their laminae. Stomata have been found in nearly all the absorbent cotyledons which have been examined; they are quite normal in appearance, and starch has been found in the guard-cells in one or two cases, where they were situated near the middle of the lamina; more commonly the stomata occurred at the apices

[1] Stomata were not distinguished, but only a single specimen was available for examination; cf. p. 405.

[2] Vide p. 407.

[3] No. 631, Bourgeau, Santa Fé, Vallé de Mexico, in Herb. Kew.

[4] For the other Mexican and Central American bulbous species, vide p. 408.

[5] Hydathodes were found in one case out of about five seedlings of *P. peruviana* examined; they were situated near the base of the lamina on the lower surface.

of these little leaves, two or three together, but in such cases no starch was seen and they thus appear to be rather of the nature of water stomata. In either case it is difficult to see that they can be of any value to the absorbent cotyledon, since its lamina is never withdrawn from the seed.

Finally, in the persistence of the primary root for some time after the formation of the bulb (cf. Figs. 7–10, Pl. XXIX, &c.), we have additional evidence of the essentially dicotyledonous character of these seedlings.

The Geophilous Habit.

The species of *Peperomia* under discussion are confined to the high mountain regions of the Andes and of Central America, and in their adult forms they show different biological adaptations, which no doubt represent their response to the peculiar xerophytic conditions of their several localities. Adaptation to new conditions must have appeared first in the adult structure of the plant, and the tendency to bulb production must be due to the shortening of internodes; but, it seems clear, from the consideration of analogous cases, that changes, leading eventually to the evolution of acaulescent forms, may take place without any appreciable effect on the structure of the seedling [1]. With further advances towards geophily, however, involving, e. g. the formation of a swollen stem-structure in definite response to xerophytic conditions, the initiation of the necessary structural modifications of the adult would begin to be thrown back more and more into the early stages of the plant's development, until finally the structure of the embryo itself would become involved.

It is obviously of paramount importance to a plant if the conditions are severe—such as, e. g., the occurrence of a long dry season—that a bulb shall be formed by the young seedling as quickly as possible, and in the most economical way [2]. We must suppose such changes to have been brought about in the seedling—which I am considering to be dicotyledonous—in response to the xerophytic conditions of the situation. The almost universal method in which this problem of bulb-formation has been solved is by the rapid transference of the reserves of the seed into the tissues of the hypocotyl, which in its turn has become adapted to receive them. The urgency of making an underground storage as rapidly as possible has no doubt been the exciting cause for a division of labour between the cotyledons. In the geophilous Peperomias, one cotyledon has been found to be capable of performing efficiently the functions of absorption [3], whilst its fellow has acquired the equally important function of

[1] Cf. Primrose, Kohl Rabi, *Plantago*, &c., &c.

[2] The special biological advantages accruing from the adoption of the geophilous habit are clearly stated by Miss Sargant in her paper, Ann. Bot., xvii, 1903, pp. 79 and 80.

[3] Cf. *Cyclamen*, where only one cotyledon is developed which absorbs the reserves in the seed, whilst the other remains rudimentary.

supplementing, during the favourable season, the reserves from the seed by means of carbon assimilation.

To adaptations of this nature may be ascribed the various known departures, from the primitive dicotyledonous type, exhibited by the seedlings of bulbous plants. A change of function accompanied by a necessary change of structure of the ordinary parts of a dicotyledonous seedling has occurred, without any suppression or non-development of the normal structures, and without the precocious development of plumular organs (cf. Text-figs. 1–9, p. 420).

In this connexion, also, these Peperomias are of particular interest, for some species have apparently reached a higher state of development and specialization than others. In *P. peruviana* the leaf-like character of the absorbent organ and the cotyledonary character of the aerial leaf are quite unmistakable (cf. Text-figs. 3 and 4, p. 420), and a somewhat similar condition of affairs is seen in *P. mexicana* and *P. pedicellata.* In *P. umbilicata*, H. B. and K., the absorbent cotyledon appears to be rather less leaf-like, and in *P. parvifolia* it has become specialized as a club-shaped organ, and has lost nearly all trace of its leafy character (cf. Text-figs. 3–6, p. 420).

There are, as is well known, examples of bulbous Dicotyledons in several other natural orders, which show pseudo-monocotyledonous modifications in the mode of germination of their seedings. These modifications have been evolved in various ways ; in some cases, perhaps, by a fusion of the two cotyledons (apparently in some Ranunculaceae), or by the abortion of one of the cotyledons (as in *Cyclamen*). All such cases are of interest when the question of the origin of Monocotyledons is considered ; for it is possible that a study of these aberrant forms may throw some light on the subject. The peculiar mode of germination of these geophilous Peperomias suggests a fresh point of view, and the interesting question is raised as to whether the evolution of the Monocotyledons from dicotyledonous ancestors may not have taken place along somewhat similar lines.

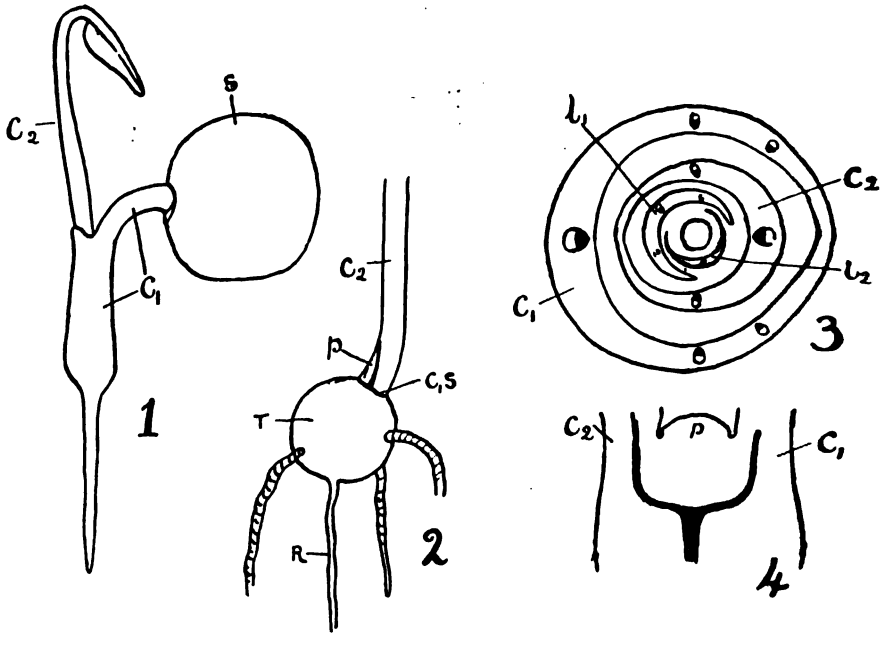
Comparison with Araceae.

Among monocotyledonous orders, the Araceae are the most nearly related to the Piperaceae [1] ; they differ from the more typical Monocotyledons in some rather important points, and, according to Scott and Sargant [2], the vascular bundle of the cotyledon in *Arum* and *Arisaema* does not show any trace of the double structure so common in the Liliaceae. In their external features, moreover, the seedlings of certain species of these two genera are strikingly similar to seedlings of the geophilous Peperomias (vide Fig. 49, Pl. XXX, and cf. Text-fig. 1, p. 418).

[1] Campbell, Ann. Bot., xiv, xv, and xix.

[2] Scott and Sargant, Ann. Bot., v, xii, Fig. 14, Pl. XXV.

In the case of the seedlings of *Arisaema Dracontium*[1], the so-called first leaf, which pushes its way through the soil with a sharply bent petiole from the base of the cotyledonary sheath, invites comparison with the aerial cotyledon of *Peperomia peruviana* or *P. parvifolia*. There is, however, one important difference between them, since the first leaf of the Aroid, together with the plumule and radicle, has been carried out of the seed at



Text-figs. of seedlings of *Arisaema* and *Arum*.

s = seed; c_1 = absorbent cotyledon; c_2 = 'first leaf' or aerial cotyledon; c_1s = scar of cotyledon; l_1, l_2 = plumular leaves; p = plumule; T = tuber; R = primary root.

FIGS. 1 and 2. *Arisaema dracontium* (after Rimbach).

1. Seedling showing the sheath of the absorbent cotyledon and the upgrowth of the so-called 'first leaf' with its sharply bent petiole.

2. An older stage, with the scar of the absorbent cotyledon. The tuber has developed, and the primary root has been displaced by contractile adventitious roots.

FIG. 3. *Arum maculatum* (after Scott and Sargant).

3. Diagram representing the course of the bundles in the epicotyledonary region of the stem, the two first seedling leaves (c_1, c_2) are seen to be directly opposite to one another.

4. *Arum sp.*, a median longitudinal section through the plumule and hypocotyl, showing the junction of the vascular bundles at the same horizontal level.

an early stage of germination, after the manner of Monocotyledons. This leaf, therefore, grows up from the base of the sheath (cf. Text-fig. 8, p. 420, and Fig. 50, Pl. XXX), and its lamina is not actually withdrawn from the seed, as in *P. peruviana*. The lamina of the 'cotyledon' is represented by the highly specialized rounded or club-shaped absorbent organ (Fig. 49 *a*, Pl. XXX), which always remains in the seed, and resembles the similarly

[1] Rimbach, Bot. Gaz., 1900, xxx, p. 174, Pl. XIII, Figs. 1 and 2.

shaped cotyledon in *P. parvifolia* (Fig. 22, Pl. XXIX). A hypocotyledonary bulb is formed in due course, and the structure of the young plant then consists, as in *Peperomia*, of the primary root, the bulb, and two opposite leaves with an undeveloped plumule (Text-fig. 2, p. 418).

Further it is of interest to notice that a median longitudinal section through the young seedling shows the two leaf-traces, from the 'cotyledon' and from the 'first leaf,' meeting below the plumule at the same horizontal level, and fusing together to form the central cylinder of the bulb and root (Text-fig. 4, p. 418).

A transverse section of a young seedling of *Arum maculatum*, in the neighbourhood of the stem-apex, shows that the midrib of the cotyledon and the midrib of the first leaf are directly opposite to one another, whilst later leaves depart from this arrangement[1], and have a very different phyllotaxy (Text-fig. 3, p. 418).

An analogous case, though still more specialized, seems to be afforded by *Tamus communis*[2]. The cotyledon has lost almost all trace of its leafy characteristics, but the first leaf, which is the only green leaf of the first year, is rapidly developed, as in *Arisaema*, and is directly opposite to the absorbent cotyledon. Similar external similarity in the mode of germination is shown by Liliaceae and allied geophilous Monocotyledons. From the foregoing considerations it seems not improbable that the absorbent cotyledon of at least some Monocotyledons is homologous with the modified absorbent cotyledon of these Peperomias, whilst the homologue of their aerial green cotyledon is to be found in the so-called 'first leaf' of the monocotyledonous seedling (Figs. 49 and 50, Pl. XXX).

The Origin of Monocotyledons.

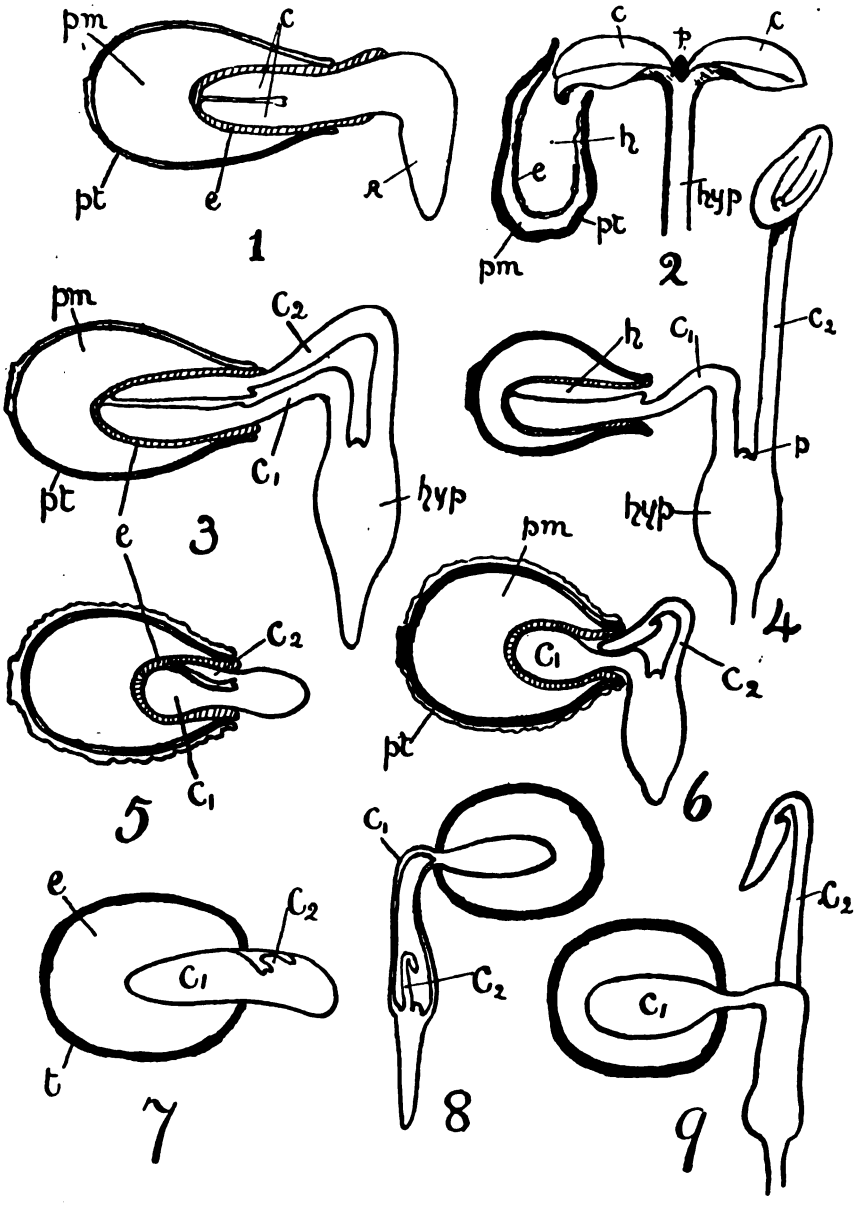
In putting forward these views of the possible origin of Monocotyledons from a dicotyledonous ancestry, suggested by the discovery of the seedlings of these geophilous Peperomias, I find myself in opposition to Miss Sargant's well-known theory[3] of the origin of Monocotyledons from a dicotyledonous stock, deduced from the anatomical study of their seedlings. According to her theory the single cotyledon of Monocotyledons is due to the fusion of the two cotyledons of the ancestral Dicotyledon, whilst in this paper evidence has been brought forward to show that the monocotyledonous habit may have been acquired by the adaptation of the two cotyledons of the ancestral Dicotyledon to different functions.

Very little in the way of anatomical evidence has been adduced to

[1] Scott and Sargant, Development of *Arum maculatum*, Ann. Bot., xii, p. 407, Pl. XXV, Figs. 11–14.

[2] Gardiner and Hill, A. W., Proc. Camb. Phil. Soc., xi, p. 445, Pl. V, Figs. 3–7.

[3] Sargant, Ann. Bot., vol. xvii, p. 1.



(See opposite page for explanation.)

Explanation of Text-figures of various seedlings in median longitudinal section.

pt = wall round the seed (pericarp and testa); *t* = testa; *pm* = perisperm; *e* = endosperm; *c* = cotyledons; c_1 = absorbent, c_2 = aerial cotyledon; *p* = plumule; *hyp* = hypocotyl; *h* = cavity in the endosperm left by the withdrawal of one or both cotyledons.

FIGS. 1 and 2. *Peperomia pellucida* (after Johnson).

1. Commencement of germination of the dicotyledonous embryo with its sheathing endosperm.
2. The two aerial cotyledons free from the seed, which is empty and shrivelled.

FIGS. 3 and 4. *P. peruviana.*

3. Slightly diagrammatic, showing the positions of the two cotyledons within the seed.
4. One cotyledon (c_1) remains within the seed, the other becomes an assimilating organ (c_2); in both cases the laminae are slightly peltate; a large cavity is left in the endosperm on the withdrawal of the aerial cotyledon.

FIGS. 5 and 6. *P. parvifolia*, diagrammatic, since part only of a seedling has been found.

5. The more complete specialization of the absorbent cotyledon (c_1) to form a club-shaped organ (cf. Fig. 22, Pl. XXIX) and the rudimentary aerial cotyledon (c_2).
6. Older seedling, showing the further development of the assimilating cotyledon (c_2), which is of very little value as an absorbent organ, and the commencement of the hypocotyledonary swelling. Only a very small cavity is left in the endosperm on the withdrawal of the aerial cotyledon.

FIGS. 7–9, a typical Monocotyledon.

7. The seed with the young embryo. The 'first leaf' or second cotyledon is very rudimentary, and is covered over by the sheath of the absorbent cotyledon. It is carried out of the seed together with the plumule and radicle.
8. The further development of the rudimentary aerial cotyledon from the base of the sheath of the absorbent organ (c_1).
9. The aerial cotyledon (c_2) has burst through the sheath of the absorbent cotyledon (c_1) and is pushing up into the air with a sharply curved petiole.

support this view, for it seems open to doubt whether such evidence is, in this case, of very definite phylogenetic value.

The Monocotyledons, at least the bulbous forms and their near allies, are a very highly specialized group of plants which, during a long period of time, have adapted themselves very successfully to xerophytic conditions with the consequent production of considerable morphological changes. It seems only reasonable to suppose that such external changes would be accompanied by corresponding modifications of the internal structure, so that possibly some of the more striking peculiarities of their internal structure may be the outcome of recent adaptations rather than the expression of developmental history.

The adoption of the bulbous habit will, of course, eventually affect the seedling structure, and the amount of modification displayed will no doubt largely depend on the length of time which has elapsed since its initiation, and the degree of perfection which has been attained. The early formation of the underground bulb is apparently essential for the geophilous plant[1], and for this purpose the absorbent organ, to be efficient, must be able to exert its influence in all directions within the seed (cf. Text-figs. 3–8, p. 420).

To bring about such a state of affairs it is necessary that at the commencement of germination all other embryonic structures shall be removed from the seed as soon as possible; hence we find the assimilating cotyledon—in a rudimentary condition—with the plumule and radicle is carried down into the ground during the first stages of germination (cf. Text-figs. 7 and 8, p. 420).

These correlated needs, acting over a long period of time, have been the powerful factor in the modification, first of the seedling structure, and finally of the embryo itself. The result of this influence has been to cause the extreme development of one cotyledon to form a pseudo-terminal absorbent organ (Text-fig. 7, p. 420), whilst the other cotyledon—the apparently lateral 'first leaf'—is left to develop from its rudiment outside the seed (cf. Text-figs. 8 and 9, p. 420).

Other Pseudo-Monocotyledonous Dicotyledons.

In certain other Dicotyledons the geophilous habit has been assumed[2], and in practically all such cases the seedlings are found to be modified in the direction of the monocotyledonous ideal.

To take the well-known case of *Cyclamen*, the monocotyledonous condition has been attained by the almost complete suppression of one

[1] e. g. seeds of *Crinum* cannot be kept for any length of time, but will germinate and produce bulbs and roots in a box without being planted in soil.

[2] A list of such plants is given by Sargant, Ann. Bot., l. c., p. 76.

cotyledon [1], the single active cotyledon functions first as an absorbent and later as an assimilating organ, and it is only under exceptional cases that the rudiment of the second cotyledon can be induced to develop [2].

Cyclamen thus appears to have worked out its own special line of evolution to a geophilous condition, which may perhaps be considered as a failure, in so far as such a method does not appear to be capable of very great possibilities [3] or to have been followed to any extent in other cases.

Another attempt at geophily with its correlated modification of the seedling structure appears to have been made by the Ranunculaceae, where a fusion of the cotyledonary petioles, and perhaps even of their laminae as well, has occurred in some cases [4], but it does not seem clear that this kind of method has been followed in the past or has led to anything more than modification within this order.

Miss Sargant, of course, contends that the anomalous Ranunculaceae, such as *Eranthis* with its fused cotyledons, afford the clue to the origin of the monocotyledonous habit of these Monocotyledons. It is certainly true that the internal structure of the cotyledonary tube of *Eranthis* [5] shows considerable resemblance to that of the 'single cotyledon' of a form like *Annemarhena* [6] which is considered by Miss Sargant to be a primitive type, but it seems an equally possible suggestion that the single median bundle of the monocotyledonous 'single cotyledon' has become divided into two bundles, in correlation in some way with the parallel venation so common to the leaves of Liliaceae, &c.

[1] Gressner, Bot. Zeit., 1874, p. 837. Darwin, Movements of Plants, p. 96; cf. Schmid, Bot. Zeit., 1902, p. 217. Gressner held the view that the embryo of *Cyclamen* was dicotyledonous with one cotyledon rudimentary, and this view is confirmed by Schmid, Taf. ix, Fig. 47, and also by my own work on various species of the genus.

[2] It is interesting to notice that the anatomical character of the petiole of the single cotyledon is suggestive of a double structure.

[3] Amongst other pseudo-monocotyledonous Dicotyledons, which may perhaps show somewhat similar modifications to *Cyclamen*, may be mentioned *Claytonia Virginica*, L.; cf. Holm, Mem. Amer. Acad. Sc., vol. x; Mem. II, p. 30, Pl. II, Figs. 10, 11, 13, 14. The 'minute leaf' figured by Holm, apparently opposite to the cotyledon, may represent the undeveloped second cotyledon. *Bunium bulbocastanum*, L., according to Hegelmaier, Vergl. Untersuch., 1878, pp. 139-140, Pl. VII, Figs. 40, 41, cf. Schmid, p. 216, has a dicotyledonous embryo, and may represent a more reduced condition than *Cyclamen*. The condition of affairs in *Erigenia bulbosa* is uncertain, vide Holm, Amer. Journ. Sc., 1901, p. 63; seedlings are at present under observation. In *Corydalis cava*, Schmid, l. c., p. 213, the second cotyledon appears to be entirely aborted.

[4] *Ranunculus ficaria* seems to afford a very good case of fused cotyledons, but a transverse section of the petiole of the 'cotyledon' shows a single entire median bundle. *R. bulbosus* also shows a slight cotyledonary tube, and *Dodecatheon* (Primulaceae), &c., also appear to be working on similar lines. In this connexion the frequent tendency to splitting among cotyledons may be referred to. This peculiarity is well seen in seedlings of *Acer pseudoplatanus*, which often appear to have three or four cotyledons; and the same thing is seen in *Primula sinensis*, where the apical depression of the cotyledon becomes a deep cut, &c. In *Cyclamen persicum* (cult.) the lamina of the single cotyledon is occasionally divided into two distinct laminae.

[5] Sargant, l. c., p. 52 et seq., Pls. VI, VII, Figs. 1-3.

[6] Sargant, Ann. Bot., xiv, p. 633, Pl. XXXIII, Figs. 2, 3; New Phytologist, i, 1902, p. 107.

The Relation of the Aroids with other Monocotyledons.

In this connexion it is perhaps worth remarking that the Aroids, e.g. *Arum* and *Arisaema*, which appear to be a more primitive and less highly specialized group than the Lilies, do not show the double bundle in the cotyledon. In *Anthurium Bakerianum*, however, there is an indication of a double bundle [1], and Miss Sargant concludes that this genus is more primitive than either *Arum* or *Arisaema*, and that it occupies an intermediate position between these genera and the Liliaceae, since it shows certain resemblances to a type like that of *Zygadenus* [2].

Miss Sargant's phylogenetic sequence [3] thus commences with a form like *Annemarhena*, and passing through *Zygadenus* and *Anthurium* terminates with the most modified forms, such as *Arum* and *Arisaema*.

A point of some interest is suggested by the fact that *Anthurium Bakerianum* shows more xerophytic characters than *Arum* or *Arisaema*, having narrow thick leaves with two lateral veins running parallel to the midrib. Thus this species may perhaps represent a more highly specialized type in the order, and in consequence shows greater modification of its seedling structures [4].

From this point of view *Arum* and *Arisaema* must be considered as simple forms allied to the Piperaceae and not very far removed from their dicotyledonous ancestors; *Anthurium*, however, owing to its more pronounced xerophily, shows an analogy in its seedlings to the more ancient group of the Lilies whose simplest and least modified forms show a more or less simple, single bundle in the cotyledon (e. g. *Zygadenus*) [5], and whose most ancient forms possess the characteristic double bundle which is seen most distinctly in *Annemarhena*.

Summary.

In conclusion some of the suggestions brought forward in the latter part of this paper may be summarized. The Ranunculaceae and other dicotyledonous natural orders show various modifications in the structure of the seedlings of some of their genera in the way of cotyledonary tubes, or in the suppression of one of their cotyledons, &c. They do not appear, however, in these examples to afford any true homology with the seedlings of Monocotyledons or to indicate the mode of origin and method of development of the monocotyledonous habit.

There can be no doubt that the study of the internal structure of the seedlings of Monocotyledons is of great value in throwing light on the

[1] Sargant, l. c., p. 45. [2] Sargant, l. c., p. 32. [3] Sargant, l. c., p. 46.
[4] Cf. Campbell, Ann. Bot., xiv, p. 21, on the primitive character of *Anthurium*.
[5] *Zygadenus* has a diarch root; cf. Sargant, l. c., p. 91, Pl. V, Fig. 12.

relationships of the various genera to one another, and possibly also of the different Natural orders; but it seems unlikely that such a study will reveal the phylogeny of the whole group, owing to its highly specialized character and the xerophytic modifications which have occurred.

The affinities between two such simple orders as the Piperaceae and Araceae appear to be much more close and definite than between the anomalous Ranunculaceae and the highly specialized Liliaceae, and in the former case the modified pseudo-monocotyledonous Peperomias show definite homologies in their adult condition with the Monocotyledons.

The geophilous Peperomias then may represent a recent attempt, by a fairly simple and possibly primitive group of Dicotyledons, to attain to the geophilous condition reached by Monocotyledons.

This attempt must be regarded as a perfectly independent development, which has happened to have worked along lines similar to those which in times past gave rise to the existing class of Monocotyledons from a dicotyledonous ancestry.

EXPLANATION OF FIGURES IN PLATES.

Illustrating Mr. A. W. Hill's paper on *Peperomia.*

Figures 1–29 have been drawn from my own material preserved in spirit, and Figs. 30–47 from herbarium material. Figs. 1, 2, 18, 24–26, 28, 29 to 31 are from photographs. The rest are from my own drawings. The natural size of the specimens is indicated alongside each figure in most cases.

PLATE XXIX.

Figures 1–17. *Peperomia peruviana,* Dahlst.

Fig. 1. A fully developed bulbous plant, showing the bulb (*cm*) with the roots springing from the sides, the peltate orbicular leaves and the inflorescences (*s*). Nat. size. A. W. Hill, no. 180, in Herb. Kew.

Fig. 2. An older specimen with a large and irregular corm and much longer petioles and inflorescences. Nat. size.

Fig. 3. A fruit in median longitudinal section, showing style and stigma (*s*); the pericarp (*p*), with its gland-cells (*g*), the testa (*t*), perisperm (*pm*), and the outline of the endosperm (*e*). Mag. × 64.

Fig. 4. A small piece of the outer layers of the pericarp, showing the slight pit with a single gland-cell. Mag. × 300.

Fig. 5. Very young seedling, both cotyledons are enclosed in the seed and there is a slight hypocotyledonary swelling. The petiole of the aerial cotyledon (*c* 2) is the more sharply bent.

Fig. 6. Slightly older seedling, the aerial cotyledon has been withdrawn from the seed; cf. Text-fig. 3, p. 402.

Fig. 7. The petiole has straightened and the peltate lamina has expanded, the absorbent cotyledon (c_1) remains within the seed.

Fig. 8. A seedling of about the same age as Fig. 7; the seed has been dissected off and the seedling placed in glycerine. The lamina of the aerial cotyledon shows three veins, whilst that of the slightly peltate absorbent cotyledon has only a single median vein. The fusion of the two cotyledonary traces below the plumule can also be seen.

Fig. 9. A young bulb or corm at the end of the first vegetative period, showing the remains of the primary root (*r*), the remains of the absorbent and the scar of the aerial cotyledon.

Fig. 10. A young plant during the second vegetative period, the corm (*cm*) is covered by hairs. The absorbent cotyledon with the seed and the remnant of the aerial cotyledon are seen. The first leaf (l_1.) has developed.

Fig. 11. A similar plant, a branched adventitious root has developed from the corm.

Fig. 12. An older plant with the third leaf developed.

Fig. 13. A young seedling, showing the relation of the two cotyledons within the seed; cf. Text-figs. 3 and 4, p. 420.

Fig. 14. Median longitudinal section through the petioles of the cotyledon and the hypocotyl (*hyp.*); the junction of the two bundles below the plumule (*pl.*) is well seen. Mag. × 300.

Fig. 15. An older plant, two green plumular leaves and several adventitious roots have developed from the tuber.

Fig. 16. Transverse section of a germinating seed about the age of Fig. 6; the remains of the pericarp and testa (*pt.*) surround the perisperm (*pm.*). This is bounded internally by the endosperm—represented by a darkly stained band—and within the cavity of the endosperm lies the lamina of the absorbent cotyledon (c_1.), its dorsi-ventral structure is still preserved and the midrib is indicated. Mag. × 120.

Fig. 17. Transverse section of the primary root at the base of the hypocotyl of a seedling similar to Fig. 7. The small diarch xylem plate consists of about two lignified elements (*x.*). *en.* = endodermis; *ph.* = phloem. Mag. × 300.

Figs. 18–28. *P. parvifolia*, C. DC.

Fig. 18. A fruit in a slightly oblique median longitudinal section, showing the short style (*s*) with the micropyle (*m*) pits in the outer layer of the pericarp with groups of gland-cells (*g*) at their bases; (*pm.*) perisperm; (*e.*) endosperm. Mag. × 64.

Fig. 19. A pit with its group of four gland-cells in a section parallel to the surface of the fruit. Mag. × 300.

Fig. 20. Two pits in longitudinal section, showing the gland-cells, with some of their contents stained by eosin. Mag. × 300.

Fig. 21. A germinated seed with the petiole of the absorbent cotyledon (c_1), the rest of the seedling has been lost.

Fig. 22. The absorbent cotyledon with its petiole and club-shaped lamina (*l.*), the seed-coats, &c. seen in Fig. 21 have been dissected away; cf. Text-figs. 5 and 6, p. 420.

Fig. 23. A young plant with the remnants of the two cotyledons (c_1, c_2), the first leaf has developed, and there is a basal tuft of roots.

Fig. 24. An older bulb with several leaf-scars and two leaves. About nat. size.

Fig. 25. A slightly older stage with well developed roots.

Fig. 26. A young bulb with an inflorescence (*s.*).

Fig. 27. A well developed plant, the corm (*cm.*) bears a terminal crown of leaves and inflorescences (*s.*) and a large basal tuft of roots. Nat. size. A. W. Hill, No. 181 in Herb. Kew.

Fig. 28. An old corm. About nat. size.

Fig. 29. *P. verruculosa*, Dahlst. The fruit in median longitudinal section to compare with that of *P. parvifolia*; the pericarp is very deeply pitted, and the innermost layer consists of large cells; the wall of the testa is thick. Lettering as in Fig. 3. Mag. × 64. A. W. Hill, No. 182, Herb. Kew.

Fig. 30. *P. umbilicata*, H. B. and K., a seedling with the seed in section; the absorbent cotyledon (c_1) is more or less club-shaped and surrounded by the endosperm (*e.*). Mexico, No. 631, Bourgeau, in Herb. Kew. Cf. Fig. 21 and Text-figs. 5 and 6, p. 420.

PLATE XXX.

Fig. 31. *P. umbilicata*, H. B. and K. A fruit in median longitudinal section, the small pits have only a single gland-cell at their base. The narrow pericarp and almost circular seed should be noted; cf. with *P. parvifolia*. Mag. × 64. Mexico, No. 802, Parry and Palmer, in Herb. Kew.

Figs. 32–41. *P. pedicellata*, Dahlst.

Fig. 32. A complete plant, showing the spherical tuber (*cm.*) with the roots springing from the upper surface, the leaves and long inflorescences (*s.*). Nat. size. No. 3829, J. Donnell Smith, in Herb. Kew.

Fig. 33. A young seedling, showing the pedicellate fruit (*f.*) and the petiole of the absorbent cotyledon (c_1), the aerial cotyledon (c_2) with its somewhat oblique primary root (*r.*), and the apogeotropic lateral root (r_1) which has become horizontal.

Fig. 34. A slightly younger seedling than Fig. 33, with the seed dissected away, showing the leaf-lamina of the absorbent cotyledon, the median primary root and the ascending lateral root.

Fig. 35. An older seedling, the lamina of the absorbent cotyledon is well seen; the primary root is slightly displaced to one side, and two secondary roots have developed (r_1, r_2).

Fig. 36. An older seedling, showing the development of the first leaf (l_1) and the lateral position of the roots.

Fig. 37. A young seedling, showing the petioles of the two cotyledons and the root-scar (*r.*) to one side of the plumule on the upper surface of the tuber.

Fig. 38. An older tuber seen from above, showing the scars of the two cotyledons, the first leaf and the apical tuft of roots (*R.*).

Fig. 39. A fully developed plant seen from the side, the absorbent cotyledon and fruit (*f.*) are still retained.

Fig. 40. A tuber like that of Fig. 39, in longitudinal section through the points of origin of stem (*p.*) and roots (*R.*); note the curved stele (*st.*) between these two points. This tuber was 1·2 mm. long by 1·8 mm. in breadth.

Fig. 41. Fruit in median longitudinal section showing the long style; the pericarp is like that of *P. peruviana*. Mag. × 64.

Figs. 42–45. *P. mexicana*, Miq.

Fig. 42. A complete plant with short tuberous rhizome (*Rh.*), scarcely peltate leaves and inflorescences. Nat. size. Mexico, No. 7,111, Galleoti, in Herb. Kew.

Fig. 43. A fruit showing the long style and peltate stigma (*st.*).

Fig. 44. A young seedling with the seed dissected away, showing the two cotyledons, the swollen hypocotyl, the primary root, and a horizontal lateral root.

Fig. 45. A similar seedling showing the leaf-like lamina of the absorbent cotyledon, the swollen hypocotyl, &c.

Figs. 46–49. *P. macrandra*, C. DC.

Fig. 46. A piece of a well developed plant with a tuberous creeping rhizome (*Rh.*), showing leaf-scars (*ls.*), and branch-scars (*bs.*), and adventitious roots; also the large glabrous peltate leaves and an inflorescence. Nat. size. Mexico, No. 4654, Pringle, in Herb. Brit. Mus. The specimens in Herb. Kew are much larger with longer leaf-petioles and long inflorescences.

Fig. 47. A flower with the bract (*b.*) and a young carpel.

Fig. 48. A young seedling, the aerial cotyledon has a large thin lamina.

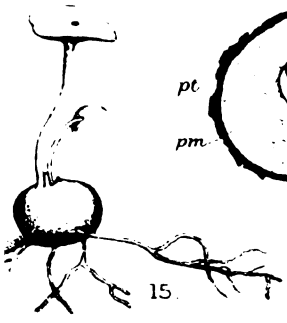
Figs. 49–50. *Arum*, sp.

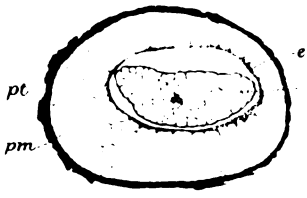
Fig. 49. A young seedling with its seed (*s.*). The 'first leaf' (c_2) has emerged from the sheath of the absorbent cotyledon (c_1). Nat. size.

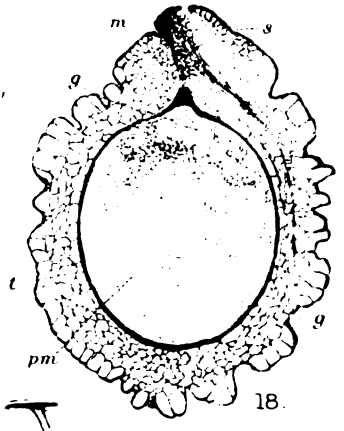
Fig. 49 *a*. The tip or modified lamina (*l.*) of the absorbent cotyledon seen in Fig. 48; cf. Fig. 22, Pl. XXIX.

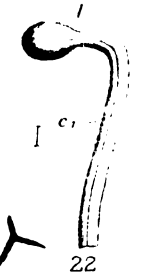
Fig. 50. The lamina of the 'first leaf'—the modified second cotyledon—of an older seedling. About nat. size.

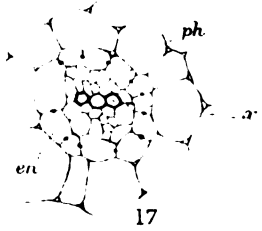
HOLL SEEDLINGS OF PEPEROMIA

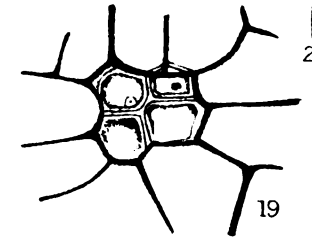


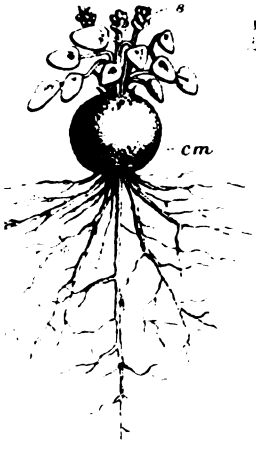


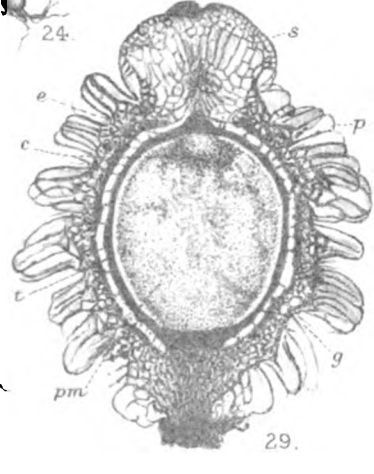


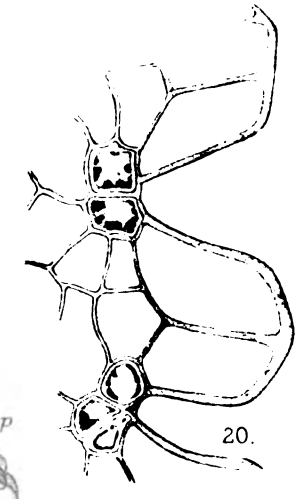


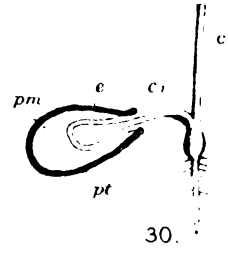






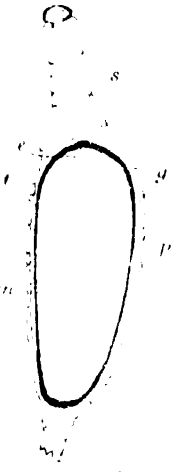


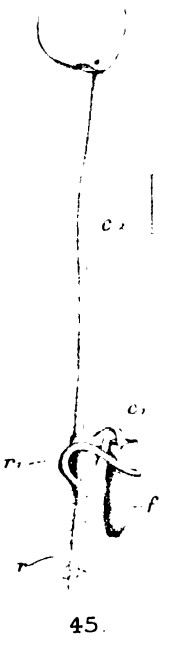


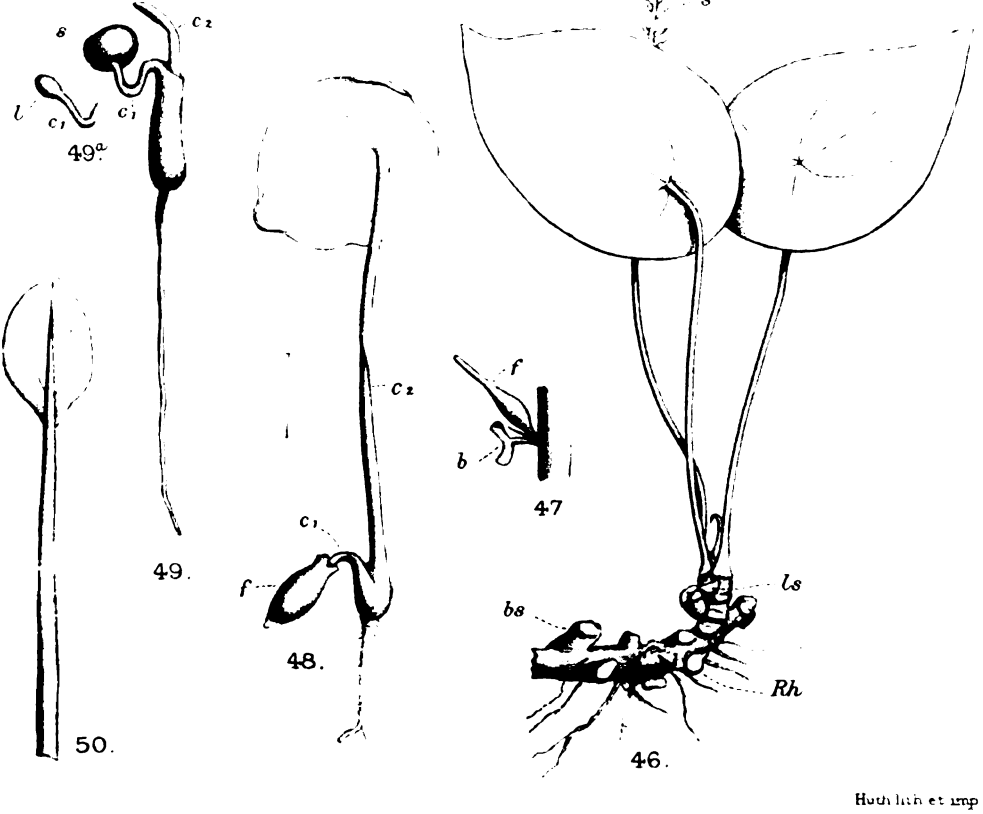


Huth lith et imp

HILL – SEEDLINGS OF PEPEROMIA.







Huth lith et imp

The 'Droppers' of Tulipa and Erythronium.

BY

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With Plates XXXI and XXXII.

I. Introduction.

In the course of Miss Ethel Sargant's examination of monocotyledonous seedlings, she noticed in the Tulip and Dog's Tooth Violet the peculiar descending stolons known to gardeners as 'droppers.' These seemed to show features of some interest, and since the question lay outside the main line of her research, she proposed to me early in 1902 that I should find out what work had been done on the subject, and try to investigate it further. I am indebted to Miss Sargant not only for suggesting this research, but also for handing over to me her *Tulipa* and *Erythronium* seedlings, and allowing me to examine her preparations of these genera. I have also to thank Mr. R. I. Lynch, M.A., of the Botanic Garden, Cambridge, and Mr. E. Aveling Green, of Berrystead, Beds, who have been most generous in supplying me with material and information. This investigation has been carried out in the laboratory of University College, and I have much pleasure in acknowledging the kind help I have received from Professor F. W. Oliver, especially in connexion with the literature.

II. The Movements of Bulbs in the Soil.

(a) *Migration.*

A great drawback of the vegetative reproduction so characteristic of bulbous plants is that it tends to overcrowding. The lateral bulbs are produced close together, and have no opportunity of colonizing fresh soil. This is got over in certain special cases by the replacement of sessile by stalked bulblets. De Vriese[1] records cases in which *Ixia lutea* and *carminosa* produced their lateral bulblets at the end of stalks from 1 to 15 centimetres

[1] W. H. de Vriese, Bydrage tot de Morphologie der Bollen, Tydschr. v. Natuurlyke Geschiedenis, Leiden, 1841.

long. Tristan [1] mentions that stalked bulblets occur in *Allium vineale*. Some Snowdrops (*Galanthus nivalis*), sent me by Mr. Aveling Green, show a similar adaptation in a very striking fashion. In *Galanthus* the growth is monopodial, the flower being produced laterally, and in these specimens the axis had elongated greatly, carrying the new bulb some little distance from the parent (e. g. Fig. 1). Mr. Aveling Green tells me that 'where they have been growing for some years in a mass, the under ones have tried to get along under the mass, and to find a way up and form a second bulb.' I have also seen exactly the same elongation of the axis in a specimen of the Snowflake (*Leucojum aestivum*), by which the new bulb was carried upwards until its base was 5·5 centimetres above the base of the parent bulb. After examining it, I came across a figure and description by Irmisch [2] of a precisely similar case in another species, *L. vernum*.

(b) *Descent.*

To each perennial plant a certain definite depth in the soil appears to be specially appropriate, and if it is disturbed it makes efforts to return to this particular level [3]. Massart [4] records a most interesting series of culture experiments on about 200 perennial species, which were planted, some at the normal level, some too deep, and some too shallow. The plants were very successful in bringing back their winter buds to the normal level by curvature of rhizomes, elongation of internodes, and so on.

To bulbous and tuberous plants a certain depth in the soil must be even more important than to ordinary perennial species, since they want protection for their succulent tissues from animals and from frost. The need for descent into the soil is especially urgent in the case of the seedling, since here the young plant starts at the surface of the ground instead of at the level of the parent bulb or corm. The commonest method of descent into the soil is by means of contractile roots [3], which are shown specially well in the *Crocus*. Here, as each successive daughter corm is formed above the parent, the need for descent is particularly obvious. The contractile root is 'always present in the young seedling, and occasionally reproduced in after years. . . . I fancy I have noticed it to be found more frequently in old Crocus bulbs when they have been brought near the surface in the process of digging a bed.' [5] The contractile roots of *Scilla*

[1] M. de Tristan, Histoire des developpemens de quelques gemmes bulbifères, Mém. du Mus. d'Hist. Nat., 1823, T. x, p. 51.

[2] M. Irmisch, Zur Morphologie der monokotylischen Knollen und Zwiebelgewächse, Berlin. 1850, p. 101, and Pl. VII, Figs. 10, 11, 12.

[3] F. W. Oliver, The Depth in the Soil at which Plants Occur, Jr. Roy. Hort. Soc., April, 1898, vol. xxi, p. 486.

[4] J. Massart, Comment les plantes vivaces maintiennent leur niveau souterrain, Bull. de la Soc. Roy. de Bot. de Belge, T. xli, 1902–3.

[5] C. Wolley Dod, Gardeners' Chronicle, 1886, p. 626.

have been investigated by Mr. Woodhead [1], both as regards their behaviour and internal structure.

Among the Lilioideae we meet with a great range of bulb structure. Perhaps the most primitive type of bulb is that of such a plant as the White Lily, in which the scales are obviously leafy, the outer ones being actually formed from the bases of the foliage leaves. A slightly more advanced stage is reached in the Turk's Cap Lily (*Lilium Martagon*), in which there are no ground leaves, and so all the bulb leaves, not merely the inner ones, take the form of specialized scales. A much more sophisticated type is that of the so-called 'tunicate bulb,' in which each scale leaf is a closed sheath, with only a small opening at the top. The most specialized methods of descent into the soil with which we are acquainted are met with in *Scilla*, *Tulipa*, and *Erythronium* among the Lilioideae, and *Gagea* among the related Allioideae, all of which have tunicate bulbs. The curious behaviour of the Wild Hyacinth is described by Rev. C. Wolley Dod as follows:—'The smallest bulbs, which I take to be the produce of the seed shed eighteen months before, in the July of the previous year, are at a depth of one or two inches, and the size of a small pea; the two-year-olds are at an average depth of four inches, and at least 70 per cent. of them are curiously elongated, being three times as long as broad. Those three and four years old—for I think some rest contented with the depth reached in the third season's growth, and some take another dive in their fourth season—are six or seven inches deep. Thus the crown of the new bulb is, on an average, 1½ inch below the base of the old one, and I feel no doubt that it is formed where it is found.' Mr. Woodhead [1] has published a full and interesting account of the life history of the Wild Hyacinth, and the structure of the curious elongated bulbs by which it lowers itself into the soil.

The most highly specialized method of descent, that by 'droppers,' is discussed in detail in the following sections.

III. Tulip 'Droppers.'

Tulip growers have long been familiar with 'droppers' ('sinkers' as they are called in Holland), and a good many accounts of them and references to them occur in horticultural and botanical literature; but it will be convenient to leave the discussion of these until after the description of my own observations.

(a) *The Non-Flowering Tulip.*

Fig. 2*a* shows a typical, immature, non-flowering plant of *Tulipa saxatilis*, in the state in which it would be found about March. The

[1] T. W. Woodhead, Notes on the Bluebell (*Scilla festalis*, Salisb.), The Naturalist, Feb. and March, 1904.

description of it applies in all essentials to the two other species of which I have had material at this stage, namely, *T. sylvestris* and *T. praecox*. The small bulb is clothed externally by a brown scale leaf. A single foliage leaf comes out of the top of the bulb, whilst a whitish stolon—the 'dropper'—and a crop of adventitious roots emerge below. If the brown scale leaf is removed, a second, and sometimes a third, scale leaf are disclosed, differing from the first in being white and succulent, but resembling it in the 'tunicate' form (Fig. 2 *b*). There may be one or more buds in the axils of the scale leaves. On removing the scale leaves and buds, the only thing left is the dwarf stem, to which are attached the roots, foliage leaf, and dropper; it is found that the latter is actually a continuation of the base of the foliage leaf (Fig. 2 *c*). It emerges from the bulb by boring its way through the scale leaves enclosing it. Sections show that the dropper is not a solid structure but a hollow tube, containing in its swollen tip a small bulb (Fig. 2 *d*). Hairs grow from the inner epidermis into the cavity of the dropper tube. The length of the dropper may be very great; a bulb of *T. sylvestris*, dug up in the middle of April, possessed one which measured $9\frac{3}{8}$ inches. Later in the year the parent bulb will be found to be dead and withered, its stored nourishment and the food manufactured by the foliage leaf having passed down the dropper into the young bulb at the tip. Eventually the dropper itself shrivels and disappears, leaving the new bulb free below.

The most reasonable view as to the morphological nature of the dropper is that it is partly foliar and partly axial, and this conception of it is confirmed by the anatomy. As the foliage leaf is tubular at the base, an axillary bud would necessarily be completely enclosed by it. The dropper is simply formed by the downward elongation of the leaf base fused on the adaxial side with the stem rudiment (Fig. 3). The tubular nature of the dropper seems to be merely a further step in the tendency to marginal fusion which is characteristic of all tulip leaves. This is shown not only in the 'tunicate' scale leaves and the bases of the ordinary foliage leaves, but also in the peculiar abnormal leaves, known as 'ascidia,' which are occasionally mentioned in the literature [1]. A complication, which has not yet been referred to, is the presence of small droppers from the axillary buds. These commonly terminate upwards in a rudimentary foliage leaf without a blade (Fig. 6 *d*). They occur chiefly in non-flowering garden Tulips, presumably forms of *T. Gesneriana*. Occasionally droppers of very curious form are found. In one specimen of *T. praecox*, I met with a dropper which, instead of running downwards, doubled sharply on itself.

[1] Germain de Saint-Pierre, Bull. de la Soc. Bot. de France, i, 1854, p. 63. Penzig, Note di teratologia vegetale, Malpighia, 16, 1902, p. 168. Miss T. L. Prankerd, B.Sc. has kindly shown me a photograph and water-colour sketch of the bulb of a pink-flowering Tulip bearing a short tubular leaf, the upper part of which was pink in colour like the flower.

and emerged from the top of the bulb side by side with the foliage leaf to which it belonged. Its tip, which was coiled like a ram's horn, contained the usual small bulb, and, in addition, there was a second one growing outside.

Since the dropper is neither purely axial nor purely foliar the question arises as to whether its region of greatest growth will be at the base as in leaves, or immediately behind the apex as in roots. To decide this, two bulbs of *T. sylvestris* were grown as water-cultures, and when they had each produced a dropper ¾ inch long, the foliage leaf and dropper in one case were divided with lines of Indian ink into zones of ⅛ inch, and in the other into zones of ¼ inch. After a few days it was found that in each the growth of the leaf was much greater in the lowest zone, and that of the dropper in the zone next behind the apex. So the growth of the dropper resembles that of the root.

I have examined the vascular transition from leaf to stem and dropper by means of serial sections (cf. Figs. 4 *e*, *f*, *g*, *h*, and Fig. 5 *b*), and also by placing the whole transition region in concentrated carbolic acid kept at a temperature just above its solidifying point. This produces sufficient transparency to allow the veins to be followed under the dissecting microscope. Fig. 2 *e* and Figs. 6 *f*, *g*, *h*, were drawn from such preparations. In *T. saxatilis* and *T. sylvestris* both these methods have been used for comparison, but in *T. praecox* the carbolic method only, and in *T. Clusiana* sections only have been employed. The anatomy is essentially the same in all four species. In general terms we may say that the bundles on the side of the cylindrical leaf base remote from the midrib run straight down to form the vascular system of the corresponding abaxial side of the dropper. The midrib and main laterals on the other hand run directly down into the stem rudiment, but each before entering it gives off a branch to supply the adaxial side of the dropper. These two sets of foliar bundles form a complete ring round the dropper. Complications are sometimes introduced by bundles starting from the stem rudiment which run a little way up into the leaf and then suddenly dive down into the dropper, or dip down into the dropper and then rise at a sharp angle into the leaf. The midrib and the main laterals of the leaf enter the dwarf stem in a crescent, but soon arrange themselves in a circle. From the side of this towards the dropper, two or more bundles as a rule send branches into the dropper, which course down its adaxial side outside the foliar vascular ring. The orientation of the bundles on the adaxial side of the dropper is very variable. The foliar bundles are inclined to place themselves so as to form, with the axial bundles, a more or less complete ring. In the dwarf stem the bundles, as we pass downwards, become concentric by the creeping of the xylem round the phloem and then fuse into an irregular plexus, which ultimately divides up completely to form the vascular systems of a crop of 3- to 5-arch adventitious roots (Fig. 5 *b*).

The droppers of *T. sylvestris* may sometimes be used for ascent, instead of descent, for Oliver (l. c.) records that when the bulbs are planted at a depth considerably below their normal level the droppers may curve upwards.

(b) *The Flowering Tulip.*

The flowering Tulip differs from the immature plants described in the last section in that the foliage leaves are produced on the flowering axis instead of growing directly from the bulb. It is obvious from this that the main bulb cannot produce a dropper as there are no ground leaves of which it can be a continuation. However, the axillary lateral bulbs sometimes produce droppers which terminate upwards in rudimentary (or occasionally normal) foliage leaves (Fig. 11).

(c) *The Seedling Tulip.*

By Miss Sargant's kindness I have been able to examine the seedlings of an unnamed species of *Tulipa* from Calcutta (Fig. 9 *a*). From the seed a long slender cotyledon emerges carrying at its tip the radicle and plumule. This tip dips down into the earth, and from it the main root and first adventitious root arise. But the shoot instead of emerging here as usual, remains inside the cotyledon tip, and by the continued elongation of the latter is carried down into the ground for some distance below the point of origin of the roots. The cotyledon thus forms a dropper to lower the first plumular bud well into the soil. I have followed the relation of the vascular system of cotyledon, dropper, and roots by means of serial sections. Miss Sargant[1] has already recorded that the transition from stem to root in this species is of the normal Tulipeae type, of which she figures *Fritillaria imperialis* as an example.

In *Fritillaria* dropper formation does not occur, so perhaps it will be well (since the dropper is the organ with which we are especially concerned) shortly to describe and figure the transition phenomena in *Tulipa* sp. (Calcutta). The cotyledon contains a pair of bundles which at the base approximate to form a double bundle with one protoxylem group (Fig. 9 *b*). The two phloem groups continue directly into the phloem groups of the diarch main root. The protoxylem group broadens into a flat plate at right angles to a line joining the centre of the two phloem groups, and the extremities of this plate form the protoxylem groups of the root. The dropper is supplied by a branch from each of the constituent bundles of the double bundle (Fig. 9 *c*). These two branches unite to form a V-shaped double bundle which presently gives off two laterals (Fig. 9 *e*). The first adventitious root arises opposite the dropper and a little below it (Fig. 9 *d*).

[1] E. Sargant, A Theory of the Origin of Monocotyledons founded on the structure of their Seedlings, Ann. of Bot., vol. xii, Jan. 1903, Pl. III, and p. 23.

(d) *The Life History of the Tulip as described in the Literature.*

The history of a garden Tulip, from the seedling stage described in the last section up to the time when it produces its brilliant parti-coloured flowers, is a very long one. For about six years [1] the seedlings do not bloom, but each season they produce a single foliage leaf above ground and a dropper below. 'The usual game of "droppers" goes merrily on, till the young bulbs feel, that if they drop any deeper, there will be suffocation through their leaves never reaching the surface alive—and they will take care not to incur this [2].' The first flowers produced are as a rule self-coloured, and the plants at this stage are known in England as 'breeders,' and on the Continent as 'Couleurs,' 'Espectanten,' or 'Muttertulpen.' After two or three years [3] the flowers may 'break' into different colours, but this process does not necessarily occur so soon. Some mother-tulips, which have been known in the self-coloured form for fifty years or more, may still occasionally 'break [4].' A change of situation, especially into a warm soil, is said to encourage 'breaking [5].' Rarely the first flowers produced by a seedling may be 'broken,' but where this occurs they do not 'break' according to the florist's rules of beauty, their colours being mixed and wanting in clearness. Sometimes 'broken' Tulips return to the plain colours of the 'breeders.' The great Haarlem bulb growers, E. H. Krelage and Sons, write to the Gardeners' Chronicle [6], 'There are a great number of varieties of Tulips, among which is a form of atavism. Occasionally some specimens lose their character and return to a form of tulip with narrow flowers, and mostly of one colour only. These Tulips are known in Holland as "thieves," and are always taken out and thrown away as of no value. We have for some years planted these variations separately and found them constant.' Solms-Laubach [4] has observed that such Tulips are especially liable to produce droppers.

Tulip droppers seem to have been repeatedly rediscovered, judging by the curiously scattered and disconnected references to them which occur in the literature. Besides the notices of them which occur in the papers of Horner, Oliver, Solms-Laubach, and Hall, already quoted, we find that de Vriese [7] refers to them in 1841, and Krünitz [8] five years later describes them as bulbs growing at the ends of root fibres. A case of droppers from the lateral buds of a mature Tulip is commented on by a writer in the Gardeners' Chronicle in 1866 [9], and another by Masters [10] in 1869. The

[1] J. G. Krünitz, Oekonomisch-technologische Encyklopädie, Berlin, 1846. And P. Miller, The Gardener's and Botanist's Dictionary, 1807.

[2] Rev. Francis D. Horner, The Florist's Tulip, Jrn. R. Hort. Soc., Jan. 1893.

[3] Krünitz, loc. cit., and A. D. Hall, The English or Florist's Tulip, Jrn. R. Hort. Soc. Sept. 1902.

[4] Solms-Laubach, Weizen und Tulpe, Leipzig, 1899.

[5] A. D. Hall, loc. cit.

[6] Gardeners' Chronicle, 1881, prt. ii, p. 182.

[7] W. H. de Vriese, loc. cit.

[8] Krünitz, loc. cit.

[9] Gardeners' Chronicle, 1866, p. 386.

[10] Masters, Vegetable Teratology, 1869.

droppers of *Tulipa sylvestris* are described in more than one place in the Gardeners' Chronicle [1] by correspondents who failed to recognize their true nature. Germain de St. Pierre [2] in 1870 and Loret [3] in 1875 refer to them as foliar structures, and compare them with the curious bulb-bearing leaves of certain species of *Allium*.

But by far the most important contribution to the subject antedates most of these references by many years. It is that of Thilo Irmisch [4] on the morphology of monocotyledonous bulbs and tubers published in 1850. This is a very valuable book, giving an accurate and exhaustive account of naked eye observations on the development and structure of bulbs. Some parts of the rather lengthy preface show that in spite of the mass of detail with which Irmisch dealt, he kept his attention fixed on the larger issues. He says, for instance, that 'Systematic Botany . . . especially in the case of the so-called higher plants, will have to rest upon comparative morphology, as Systematic Zoology has comparative anatomy for its essential basis,' and he adds 'It would rejoice me greatly if my observations should be found not useless as material for a scientific systematic treatment of (of course) only an extremely small number of plant species.' Irmisch's descriptions and figures of the immature Tulip-bulb and its dropper are so good that they may be felt to render the present paper unnecessary. My excuse is that Irmisch's work seems unfamiliar to many botanists, and that in his account of the droppers (which is confined to those of *T. sylvestris*) he does not figure the seedling or the flowering bulb, and he leaves the anatomy out of consideration. In his own words 'The morphology of fully developed plants like the comparative anatomy of fully developed animals will generally lead to sure results without reference to knowledge of tissues. Still cases arise in which the knowledge of the anatomical structure of a part will be valuable for the determination of its morphological significance.' As a matter of fact my examination of the anatomy has simply confirmed Irmisch's view as to the morphology of the dropper, namely, that it is formed partly of an elongation of a portion of the axis and partly of an invagination of the sheathing or dorsal surface of the leaf.

IV. Erythronium 'Droppers.'

Irmisch [5] has given a full illustrated description of the structure and development of the bulb of *Erythronium Dens-canis* in which the seedling

[1] Gardeners' Chronicle, May and Sept. 1888.

[2] Germain de Saint-Pierre, Nouveau Dictionnaire de Botanique, Paris, 1870.

[3] Loret, Sur les bulbes pédicellés du *Tulipa silvestris*, Bull. de la Soc. Bot. de France, T. xxii, 1875, p. 186.

[4] T. Irmisch, Zur Morphologie der monokotylischen Knollen und Zwiebelgewächse, Berlin, 1850, p. 57, and Plate V, Figs. 12–22.

[5] Th. Irmisch, Beiträge zur vergleichenden Morphologie der Pflanzen, Abhandl. der Naturforsch. Gesellsch. zu Halle, Bd. VII, Heft iii, 1863, p. 184.

possesses a well-marked dropper; in the succeeding years, however, the outgrowth is so rudimentary as scarcely to deserve the name. The structure of the bulb closely resembles that of the Tulip, and the non-flowering plant produces annually a single foliage leaf. Asa Gray[1] refers to the 'subterranean runners' of *E. americanum* and *E. albidum*, and figures another species *E. propullans*, in which a similar structure arises from a point some little distance *above* the parent bulb. It would be interesting to know what the exact morphology is in this case. F. H. Blodgett[2] gives a very telling series of figures of *E. americanum*, illustrating the five-year cycle from seed to flowering plant, and showing the amount of dropping that occurs each season. My Figs. 7 and 8 show two stages in the development of a young dropper in this species.

I have examined the seedling structure of another species, *E. grandiflorum*, by means of serial sections through the transition region of a seedling nineteen days old (Fig. 10). Miss Sargant[3] has already mentioned that *E. Hartwegi* has three bundles in the cotyledon which form a triarch root according to the first type of transition described by V. Tieghem. In one of the two seedlings of *E. grandiflorum* which I sectioned, the cotyledon near its base contained a midrib with two laterals, and immediately inside the midrib there was a small inverted bundle (Fig. 9 *b*). The laterals and the small inverted bundle pass down directly into the dropper and have no bearing on the symmetry of the root. The phloem mass of the midrib runs straight down to form one of the phloems of the triarch root. The xylem of the midrib gives rise to two of the xylem poles of the root, while the third, as well as the two remaining phloem groups, are supplied partly by it and partly by the chief bundle of the dropper (Fig. 9 *d*). The latter is a double bundle with a single xylem group and two phloems, and occupies the position in the dropper corresponding to that of the midrib in the leaf. There are six bundles in the transverse section of the dropper (Fig. 9 *e*): the midrib which connects with the root, the two laterals which are continuous with the laterals of the cotyledon, the small inverted bundle which also continues right into the cotyledon, and one bundle on each side arising as a branch of the cotyledon midrib. By the outward migration of the small inverted bundle a ring of bundles is formed in the dropper in place of the comparatively leaf-like arrangement in the cotyledon. The second seedling which I cut differed from this one in the absence of the small inverted bundle.

[1] Asa Gray, A New Species of *Erythronium*, Amer. Nat., 1871, p. 298.

[2] F. H. Blodgett, Vegetative Reproduction and Multiplication in *Erythronium*, Bull. Torrey Bot. Club, xxvii, p. 305.

[3] E. Sargant, loc. cit.

V. Gagea 'Droppers.'

The droppers of *Gagea arvensis* are figured by Irmisch [1]. They recall those of *Tulipa* and *Erythronium*, but are exceedingly short, so that the new bulb is carried a very little distance down into the ground.

VI. Summary.

The power of lateral migration to prevent overcrowding, and of descent into the soil for protection against frost, drought, and animals, is possessed in some degree by many bulbous plants. The most specialized methods of downward migration are those of certain 'tunicate' bulbs, *Scilla*, *Gagea*, *Tulipa*, and *Erythronium*. The last three produce the structures known as 'droppers.' In *Tulipa* and *Erythronium*, with which we have been particularly concerned in this paper, the immature bulb each year produces a single foliage leaf continued at the base into a hollow tube, the 'dropper,' enclosing a bulb at its tip. Irmisch's interpretation of this as partly axial and partly foliar is borne out by its anatomy. The region of greatest growth in the dropper is immediately behind the apex, showing that this foliar-axial organ has become root-like in more than mere externals. Both immature and flowering Tulips may produce droppers from lateral buds. *Tulipa* and *Erythronium* are much alike in almost every point, including the structure of the bulb and the external morphology of the seedling, and they are regarded by systematists as closely related, but the type of seedling anatomy in the two genera is curiously different. *Tulipa* conforms to the normal Tulipeae type, while *Erythronium* is aberrant. In the latter genus there are at least three bundles in the cotyledon, and this is correlated with a triarch root, while *Tulipa* has only two bundles in the cotyledon together corresponding to the midrib of *Erythronium*, and a diarch root. The triarchy of the *Erythronium* main root may possibly be connected with the fact that the plant depends on it alone for some time, whereas in *Tulipa* a second root is produced almost immediately.

Note. Since the above paper was written my attention has been called to an important treatise in Danish by Christian Raunkiær, 'De Danske Blomsterplanters Naturhistorie,' Bd. I, Copenhagen, 1895–9. The author figures and describes external views and dissections of immature dropper-bearing plants of *Tulipa sylvestris*. He also figures a case of elongation of the axis in a bulb of *Galanthus nivalis* (Fig. 104 F) similar to that shown in my Fig. 1. He further describes and figures the peculiarities of bulb formation in a number of species of *Gagea*.

September 17, 1906.

[1] Th. Irmisch, loc. cit., 1850, Pl. IV, Figs. 22, &c.

EXPLANATION OF PLATES XXXI AND XXXII.

Illustrating Miss A. Robertson's paper on the 'Droppers' of *Tulipa* and *Erythronium*.

f. = foliage leaf; *d.* = *dropper*; *d.b.* = tip of dropper containing bulb; *d.w.* = dropper wall; *sc.* = scale leaf; *l.b.* lateral bulb; *st.* = dwarf stem; *v.b.* = vascular bundle; *m.r.* = midrib; *d.m.r.* = dropper mid-rib; *d.v.b.* dropper vascular bundle; *x.* = xylem; *ph.* = phloem; *r.* = main root; r_1. = first adventitious root; *adv. r.* = crop of adventitious roots; *c* = cotyledon.

PLATE XXXI.

Fig. 1. Bulb of *Galanthus nivalis* (June, 1903) showing prolongation of axis, and formation of new bulb some little distance from parent (Nat. size).

Fig. 2. Non-flowering plant of *Tulipa saxatilis* (March, 1902).

Fig. 2 *a*. Whole plant ($\frac{3}{4}$ nat. size).

Fig. 2 *b*. Bulb with outer scale leaf removed (Nat. size).

Fig. 2 *c*. Bulb with inner scale leaf and axillary bulb removed, showing continuity of base of foliage leaf and dropper (Nat. size).

Fig. 2 *d*. Longitudinal section of tip of dropper showing bulb (slightly enlarged).

Fig. 2 *e*. Transition region of foliage leaf, stem, and dropper in carbolic acid to show veining (slightly enlarged). Three main veins run up the back of the leaf from the stem base. The bundles supplying the adaxial side of the dropper all arise as branches from these three.

Fig. 3. Diagram to represent the mode of origin of the dropper of *Tulipa* by invagination of the tubular base of the foliage leaf fused on one side with an outgrowth from the stem. The stem is distinguished by cross-hatching.

Fig. 4. *Tulipa Clusiana* (December, 1903).

Figs. 4 *a*, *b*, *c*, *d*. Stages in the dissection of the bulb (Nat. size). Fig. 4 *d*. shows a small dropper forming the continuation of the foliage leaf. Also a lateral bud.

Figs. 4 *e*, *f*, *g*, *h*. Diagrams of sections cut at the levels marked by these letters in Fig. 4 *d*. The bundles are not yet completely differentiated into xylem and phloem (× 13 *circa*).

Fig. 4 *e*. Section at the level at which the tabular cavity of the leaf base opens to the exterior.

Fig. 4 *f*. Section near top of lateral bulb.

Fig. 4 *g*. Section through attachment of lateral bulb. Bundles are passing from the stem into the dropper.

Fig. 4 *h*. Dropper free from stem. Note circle of bundles on adaxial side. Bundles in stem rudiment are becoming irregular.

Fig. 5. *Tulipa saxatilis* (March, 1902).

Fig. 5 *a*. Central part of bulb showing rudimentary stem to which is attached base of foliage leaf, dropper, and adventitious roots (Nat. size).

Fig. 5 *b*. Section at the level marked *B* in Fig. 5 *a*, showing dropper and bases of numerous 3- to 5-arch adventitious roots, embedded in the rudimentary stem.

Fig. 6. *Tulipa praecox* (March, 1902).

Figs. 6 *a*, *b*, *c*, *d*, *e*. Dissection of bulb by removal of successive scale leaves. This bulb has a dropper in connexion with its foliage leaf, and also a second dropper from a lateral bulb. The second dropper is slightly connected with the outer tissues of the first.

Figs. 6 *f*, *g*, *h*. Three views of the transition region of the leaf and main dropper in carbolic acid (slightly enlarged). Five veins on the midrib side of the leaf run straight into the stem rudiment, and four veins on the sheathing side run straight into the abaxial side of the dropper. The fifth vein on the sheathing side of the leaf connects with an arch from the stem rudiment, and does not continue down into the dropper. Some veins come straight from the stem rudiment and run down into the back of the dropper which is also partly supplied by branches from the five main leaf veins.

Fig. 6 *k*. Apex of second dropper in carbolic acid (slightly enlarged).

Figs. 7 and 8. *Erythronium americanum.*

Figs. 7 *a* and *b*. Young bulb (February, 1904). Fig. 7 *b*. Longitudinal section showing lateral bulb within the tubular base of the foliage leaf which will later form a dropper.

Fig. 8. Older bulb (April, 1904). Two droppers have grown out.

PLATE XXXII.

Fig. 9. *Tulipa sp.* (Calcutta).

Fig. 9 *a*. Seedling (Nat. size).

Figs. 9 *b*, *c*, *d*, *e*. Transverse sections showing the vascular connexion of cotyledon, main root, and dropper (× 146).

Fig. 9 *b*. Cotyledon near base showing two bundles with a common protoxylem group. Outer parenchyma and epidermis omitted.

Fig. 9 *c*. A little lower than Fig. 9 *b*, showing a branch going off to the dropper from each limb of the double bundle.

Fig. 9 *d*. Diarch root on the right formed from the main part of the cotyledon double bundle, and dropper vascular system on the left formed from the two branches named *d. v. b.* in Fig. 9 *c*. These at first unite into a V-shaped double bundle, which in this section is beginning to divide up. On the right the first adventitious root is coming off.

Fig. 9 *e*. Dropper and root quite separate. The vascular system of the dropper now consists of a midrib and two laterals.

Fig. 10. *Erythronium grandiflorum.*

Fig. 10 *a*. Seedling. *s* = seed. (Nat. size.)

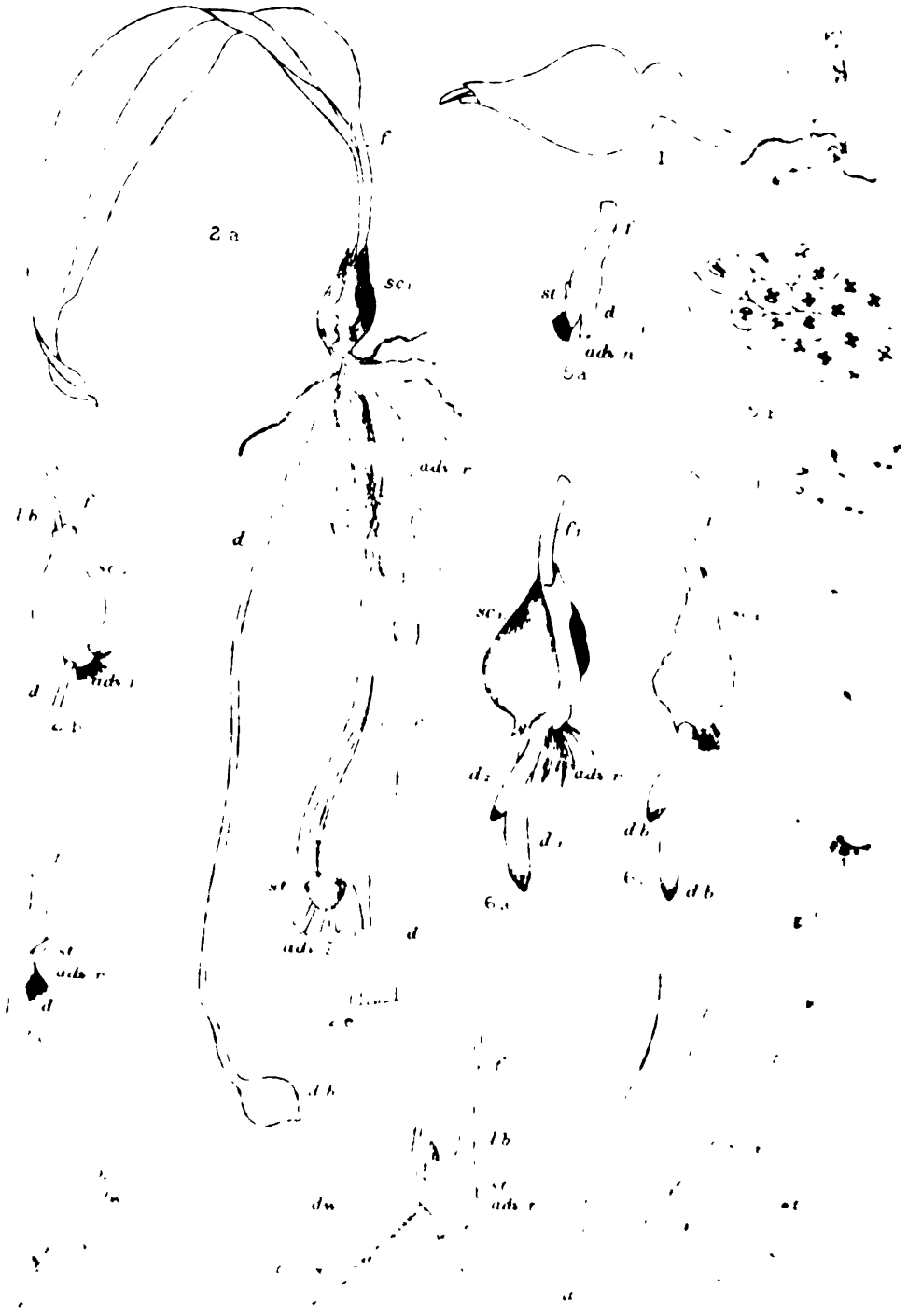
Figs. 10 *b*, *c*, *d*, *e*. Transverse sections showing relation of vascular system of cotyledon, root, and dropper. Outer parenchyma and epidermis omitted. *i. v. b.* = inverted vascular bundle; l_1 and l_2 = lateral bundles (× 146).

Fig. 10 *b*. Near base of cotyledon.

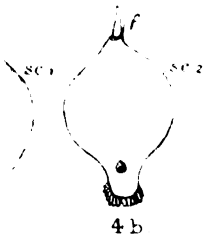
Figs. 10 *c* and *d*. Transition region. *d.m.r.* = dropper mid-rib.

Fig. 10 *e*. Triarch root completely formed to the right and dropper vascular system to the left. *r. c.* = root cylinder.

Fig. 11. *Tulipa sp.* (*Gesneriana ?*). Flowering tulip with a dropper from one of its lateral bulbs (July, 1906). *f. st.* = flowering axis. (⅓ nat. size.)

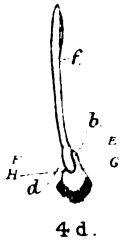


ROBERTSON DROPPERS OF TULIPA AND ERYTHRONIUM



4b.

4c.



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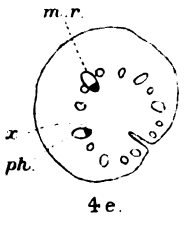
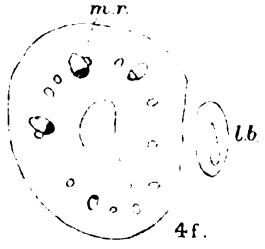
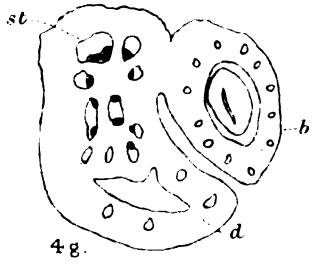


4e.



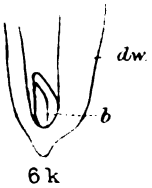
4f.



4g.

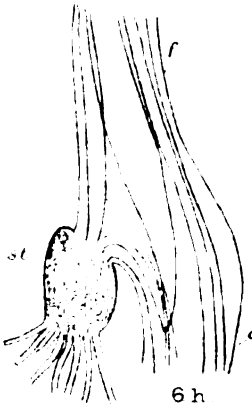
4h.

6e.



6k.

7a.



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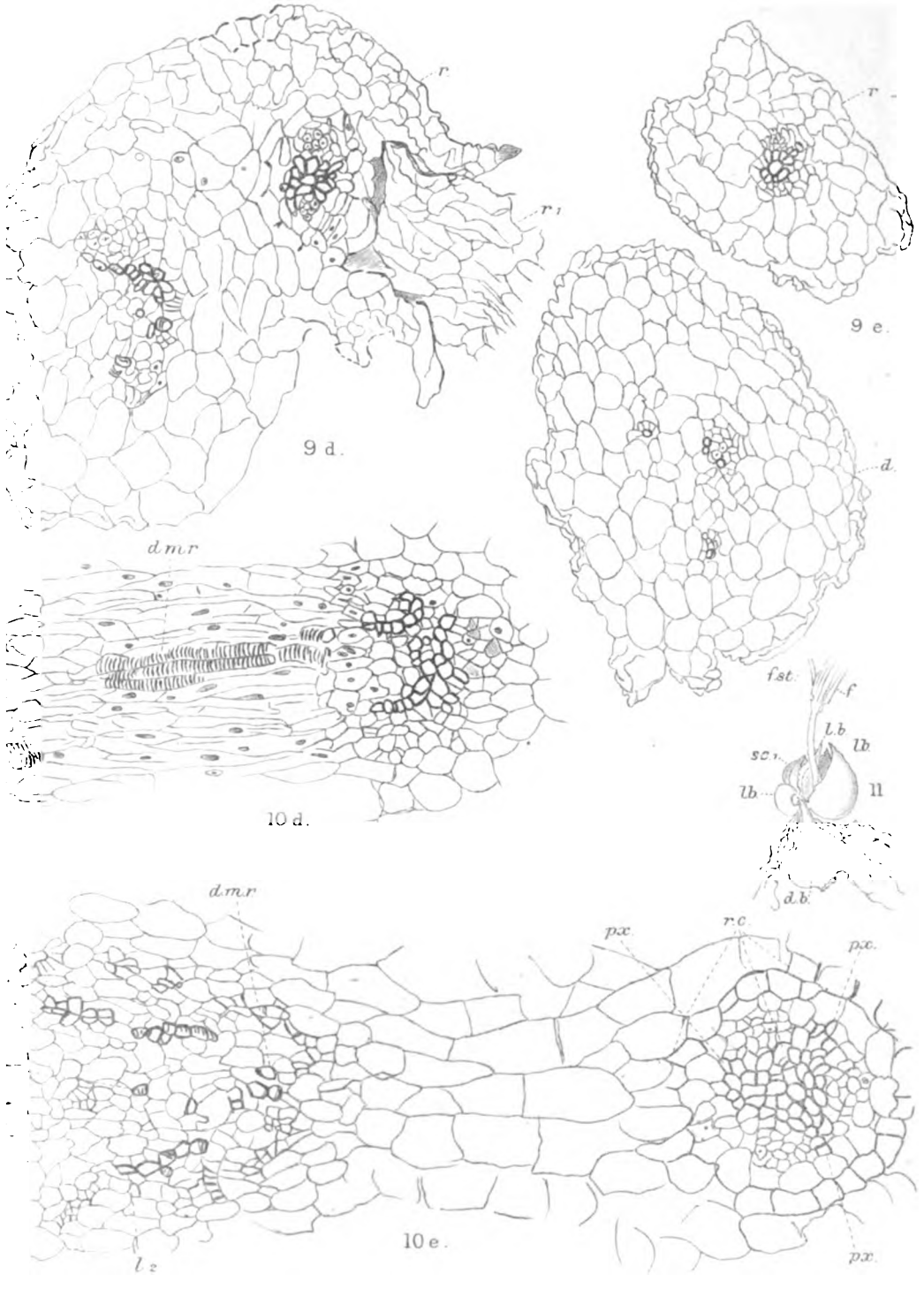
8.

7b.

ROBERTSON DROPPERS OF TULIPA AND ERYTHRON M



Huth lith et imp.

Bartonia, Muehl. An Anatomical Study.

BY

THEODORE HOLM.

With Plates XXXIII and XXXIV.

IN systematic works dealing with Gentianeae, *Bartonia* and *Obolaria* are invariably placed side by side on account of the following characters: 'Lobes of the corolla imbricated in the bud, i. e. two exterior and two interior; no appendages; ovules and extremely numerous, minute, close-coated seeds covering the whole parietes of the ovary and capsule; stamens inserted in or little below the sinuses of the corolla; anthers ovate-sagittate; foliage hardly any or discoloured' (Gray: Synoptical Flora of North America). Or 'corolla efoveolata, lobis imbricatis' (Bentham et Hooker). A like characterization is offered by Gilg (Natürl. Pflanzenfam. iv, 2), but with the additional remark: 'Schwachgrüne Halbsaprophyten.' By Bentham, Hooker, and Baillon these genera are placed among the Swertieae, by Gilg among the Erythraeinae.

In regard to *Obolaria* the writer has, some years ago, described some of the most salient points in its external and internal structure[1], and we have shown that the corolla does possess nectaries in the shape of small, fringed scales, besides that the plant contains chlorophyll in abundance, and that the corallioid roots represent mycorhizae. In habitus the genus differs very much from *Bartonia*; it is a rather robust plant in proportion to its size, and the fleshy leaves are very conspicuous. In *Bartonia*, on the other hand, we meet with plants of exceedingly slender habit, threadlike stems and minute, subulate leaves. Common to both is the presence of chlorophyll and corallioid mycorhizae.

When Gray (l. c.) described *Bartonia* only two species were known: *B. verna*, Muehl. and *B. tenella*, Muehl., the latter with a variety *Moseri*. Since then two more species have been established, viz. *B. lanceolata*, Small[2], and *B. iodandra*, Robins[3]. Characteristic of the latter is the colour of the anthers, being sometimes purplish or dark maroon, besides the calyx being

[1] Annals of Botany, vol. xi, no. xliii, September, 1897, p. 369.
[2] Flora of the South-eastern United States, 1903, p. 932.
[3] Botan. Gazette, 1898, p. 47, and Rhodora, vol. ii, p. 56.

[Annals of Botany, Vol. XX. No. LXXX. October, 1906.]

turbinate below. The former, *B. lanceolata*, is characterized by possessing lanceolate corolla-lobes, which are entire, acute or acuminate, in contrast to *B. tenella* in which the corolla-lobes are oblong and erose; but the differences in the structure of the stigma are not mentioned. In regard to the geographical distribution of these species, *B. verna* occurs in the southern States from S. Virginia to Florida and Louisiana; *B. tenella* and *B. lanceolata* are widely dispersed in the Atlantic States from Connecticut to Florida. west to Wisconsin and Arkansas; while *B. iodandra* is a more northern plant, having been found only in Newfoundland, Nova Scotia, and Massachusetts. In the District of Columbia and Maryland *B. lanceolata* is the only species that has been observed by the writer. It would thus appear as if *B. verna* and *B. iodandra* occupy a more distinct geographical area than the others, even if these have not, so far, been found directly associated with each other.

In regard to the specific merits of these four plants, *B. verna* is perhaps the most constant and the most readily distinguished. Besides being vernal (the three others are autumnal), the pure white corolla and the compressed ovary make it very distinct. The lobes of the corolla are spreading (Plate XXXIII, Fig. 1), one-nerved, obtuse and very minutely erose (Fig. 2): the stigmatic surface (Fig. 4) of the ovary is long and very prominent. In *B. lanceolata* the corolla-lobes are erect (Fig. 9), lanceolate, more or less involute along the margins, and three-nerved (Fig. 7), besides that the colour is yellowish to white; the ovary of this species (Fig. 10) is quadrangular in cross-action, and the stigmatic surface very small, not extending beyond the corolla (Fig. 9). In *B. tenella*, on the other hand, the lobes of the corolla (Fig. 18) are oblong, obtuse, erose and three-nerved, and the colour is frequently more or less purplish; the stigmatic surface (Fig. 19) is very conspicuous and raised above the corolla (Fig. 17). Intermediate between *B. lanceolata* and *B. tenella* is the little-known *B. iodandra*, in which the flesh-coloured corolla-lobes are broadly oblong and obtuse, while the stigmatic surface is small and does not reach beyond the corolla. The flowers are usually somewhat larger than those of *B. tenella*, and the calyx is, as already stated, turbinate below. It may be that *B. iodandra* represents a mere geographical form of *B. tenella*.

The inflorescence is a cyme in all the species, but often somewhat irregular on account of the leaves being, sometimes, not exactly opposite, and this is especially the case with *B. iodandra*, besides in weak, few-flowered specimens of *B. lanceolata* (Fig. 5). Small, one-flowered specimens of *B. verna* are common, while the largest number of flowers observed in this species is nine; but three-flowered individuals appear to be the most frequent. In *B. tenella* and *B. lanceolata* (Fig. 6) the inflorescence is often ample and rich-flowered.

Characteristic of these species are the minute, appressed leaves, normally

opposite, but very frequently not so; in vigorous specimens of *B. tenella* and *B. lanceolata* they are often quite crowded and strictly opposite at the base of the stem. The root-system is poorly developed and only represented by some few slender, secondary roots, there being no primary. The germination seems to be unknown.

In regard to the internal structure our genus is very little known, and no mention has been made in Dr. Solereder's comprehensive work on the Anatomy of Dicotyledons[1]. Nevertheless the structure has been touched upon, though very briefly, by W. Bötticher[2] and E. Perrot[3] in their treatments of the Gentianaceae. These plants are, as a matter of fact, very difficult to study from dried and pressed material alone, and since the writer has been able to obtain fresh specimens of *B. verna* and *B. lanceolata*, we take the opportunity to present the following results of our anatomical investigation, concerning the vegetative organs.

BARTONIA VERNA, Muehl.

The Roots.

As stated above, the roots are mycorhizae; they are somewhat fleshy, sparingly branched, and lack hairs; they are not contractile. A thin-walled epidermis covers directly the cortical parenchyma, no exodermis being developed. The cortex consists of about six compact layers, in which fungal hyphae are very frequent. Endodermis is thin-walled, and shows the Casparyan spots very plainly. The thin-walled, continuous pericambium surrounds two groups of leptome, alternating with two rays of hadrome, and the narrow vessels extend to the centre of the root. Other roots were observed to be triarchic.

The Stem.

The basal internode is cylindric, glabrous and smooth. A thick, wrinkled cuticle covers the epidermis (Plate XXXIII, Fig. 11), of which the external and radial cell-walls show a very pronounced thickening; some stomata were observed (Fig. 11), and they were level with the surrounding epidermis. Inside the epidermis is a cortical parenchyma of about nine layers of thin-walled cells with narrow but distinct intercellular spaces. The cells of the cortex contain a little chlorophyll and are of about the same size throughout, but only the innermost strata are arranged radially, although no endodermis was observed. The cortex borders thus directly on the mestome-strands, the structure of which is very irregular, there being about ten groups of leptome, but an almost continuous ring of hadrome, besides four leptomatic strands, located in the pith. The innermost

[1] Systematische Anatomie der Dicotyledonen, 1899.

[2] Beiträge zur vergleichenden Anatomie der Gentianaceen. Inaug. diss. Erlangen, 1895, p. 55.

[3] Anatomie comparée des Gentianacées. Thesis. Paris, 1899, p. 192.

portion of the stem is occupied by a thin-walled but compact pith with no deposits of starch.

If we examine one of the internodes from the middle of the stem, the structure is somewhat different. The cross-section is quadrangular, and stomata are more frequent (Plate XXXIV, Fig. 23); they are surrounded by four cells. A typical, thin-walled endodermis is differentiated in this part of the stem, but otherwise the structure of the cortex and epidermis is identical with that of the basal internode. The mestome-bundles are very irregular (Plate XXXIV, Fig. 20), some being bicollateral, others being reduced to a small group of vessels, bordering directly on the endodermis (Fig. 24), and the hadrome does not here form a closed ring around the pith. We noticed six groups of leptome in the pith, and these were more or less separated from the hadrome, as may be seen in our figure (24).

In the apical internodes we notice the same structure and the same irregular development of the mestome-bundles. For instance, as shown in Fig. 12, pure leptomatic strands occur within the endodermis, or the mestome-bundles may be strictly collateral, though exceedingly small, as figured on Plate XXXIII, Fig. 13.

It thus seems characteristic of this species that the stem lacks mechanical tissues, stereome and collenchyma, and that epidermis is the only tissue that has acquired some strength and firmness by the thickening of the cell-walls.

The Leaf.

All the leaves of *Bartonia verna* are minute, subulate and appressed to the stem; they are triangular in cross-sections with a keel on the dorsal face. The cuticle is thick, wrinkled on both faces of the blade. Viewed *en face*, the cells of epidermis are rectangular with the radial walls slightly undulate; in transverse sections the cells on the dorsal face are conspicuously larger than on the ventral; the outer cell-wall is moderately thickened on both faces. Stomata surrounded by four cells were observed on both faces, but they are most frequent on the dorsal. The chlorenchyma represents a homogeneous tissue of roundish cells loosely connected, and often traversed by a lacune near the centre; chlorophyll, but only in small quantity, was observed. There is only one vein, located in the keel; it consists of a small mestome-strand, destitute of mechanical support, and has no parenchyma-sheath either. The elements of the leptome are very small, and the hadrome contains only a few, narrow vessels.

Glandular hairs of the same structure as those which we observed in *Obolaria* (l. c.) were noticed at the very base of the leaves, but only on the ventral face.

BARTONIA LANCEOLATA, Small.

The Roots.

The roots are short and slender, sparingly branched and of a brownish colour; no hairs were observed. Hyphae were found in epidermis, exodermis, and in all the cells of the cortex. Inside epidermis is a single layer of thick-walled cells representing an exodermis. The cortex consists of three strata of large, roundish cells with wide intercellular spaces. It borders on an endodermis, the cells of which are thin-walled and much smaller than those of the cortex proper; the Casparyan spots were plainly visible. A thin-walled, continuous pericambium surrounds three small strands of leptome alternating with three rays of hadrome, the vessels of which are very narrow. Some other roots that were still thinner contained only two leptome-strands and two hadromatic rays.

Although the majority of roots examined proved to be mycorhizae, we did observe a few in which no hyphae were to be traced. The structure of these roots agreed, however, with that of the others, but the epidermis showed here a tendency to develop low papillae, the exodermis was quite thin-walled, and the tissues showed a more regular structure and arrangement than observed in the mycorhizae.

The Stem.

One of the basal, cylindric internodes shows the structure as follows: A wrinkled cuticle covers the epidermis, the outer cell-walls of which are moderately thickened; no stomata were observed, the internode being underground. No exodermis is differentiated, thus the cortex borders directly on epidermis; the cortical parenchyma consists of seven layers in which the intercellular spaces are quite wide; no chlorophyll or starch was noticed. There is, furthermore, an endodermis (Fig. 22), mostly thin-walled, or some of the cells showed a thickening all around, but only outside the leptome. A continuous ring of thick-walled cells separates the leptomatic strands from the hadrome, thus forming a protective sheath around the hadromatic cylinder. The cells of this sheath are, in longitudinal sections, longer than those of endodermis, and their cross-walls are straight and horizontal; they are of a lighter colour than the vessels, and the walls are porous. Morphologically the elements of this protective sheath may be defined as representing thick-walled mestome-parenchyma rather than modified sclerenchyma. In regard to the leptome this tissue occurs as isolated strands, about ten in all, bordering directly on endodermis. The hadrome, on the other hand, forms a closed cylinder of vessels in several layers, wide reticulated and narrower scalariform. The central portion of the internode is occupied by a solid but thin-walled pith, in which no

deposits of starch were observed. In this pith are located about eight leptome-strands, which are not arranged so as to correspond radially with the peripheral leptome, and they all are separated from the hadrome by layers of parenchyma pertaining to the pith.

A somewhat different structure is to be observed in the lowermost of the aerial internodes, a short distance above the one described in the preceding. The internode is obtusely quadrangular in cross-section, and stomata occur; these are level with epidermis and surrounded by four cells (Fig. 21). The cortical parenchyma is here composed of only three strata, which contain chlorophyll, and the intercellular spaces are very wide. Endodermis is very thick-walled and porous, and surrounds a central cylinder of the same constituents as described above, and arranged in the same way. The mestome-parenchyma is, however, more thick-walled than observed in the subterranean internodes, and the mestome represents now about eight distinct bicollateral mestome-strands, instead of a confluent mass of hadrome and isolated leptome, the innermost groups of which border here almost directly on the hadrome. The pith shows the same structure as above, but extends now between the hadrome to the protective sheath.

This same structure was observed in all the other internodes above, but the cross-section becomes gradually more sharply quadrangular, and at the same time the number of peripheral leptome-strands becomes reduced to only four outside the several groups of hadrome with leptome on the inner side.

In the peduncles of the flowers we noticed a corresponding structure, and chlorophyll was observed in the guard-cells of the stomata and in the cortex. The peduncle is sharply quadrangular, and contains a thin-walled endodermis, surrounding a central cylinder with four broad strands of leptome corresponding with the four angles, besides a sheath of thick-walled mestome-parenchyma as above. The hadrome forms an almost closed ring with about five internal strands of leptome, and a central, thin-walled pith without starch.

The Leaf.

The leaves are of the same shape and small size as those of *B. verna*, and possess the same kind of glandular hairs as observed in this species. A transverse section of the leaf (Plate XXXIII, Fig. 16) shows a smooth cuticle and a moderate thickening of the outer cell-walls of epidermis. Stomata level with epidermis occur on both faces of the blade. The chlorenchyma constitutes a homogeneous tissue of roundish cells, which contain chlorophyll; the intercellular spaces are narrow, and no lacunes were observed. No stereome is developed, and the single mediane vein possesses no parenchyma-sheath, but only a very few leptome-cells and narrow vessels. The leaf-structure is thus almost identical with that of *B. verna*.

In comparing these two species with each other, we notice the following anatomical characters, by which they may be distinguished :

Root without exodermis, *B. verna.*
„ with thick-walled „ *B. lanceolata.*
Stem without sheath of mestome-parenchyma, *B. verna.*
„ with „ „ thick-walled „ *B. lanceolata.*
Leaf with wrinkled cuticle and very open chlorenchyma, *B. verna.*
„ „ smooth „ „ compact „ *B. lanceolata.*

Our genus has thus several histological features in common with *Obolaria* (l. c.), and we notice especially the root-structure, that of a typical mycorhiza, common to both. Moreover, the stem of *Obolaria* possesses also an endodermis, and shows, like *Bartonia*, the complete absence of stereome ; the mestome-strands are also bicollateral. But the foliage of *Obolaria* is better developed, the leaves being larger and quite fleshy ; nevertheless the structure is much the same, the chlorenchyma being only represented by a homogeneous tissue of roundish cells with no indications whatever of palisade-cells. In regard to the floral structure, the corolla of *Obolaria* shows the presence of nectaries, which do not occur in any of the species of *Bartonia.*

The fact that the roots are mycorhizae might indicate that these genera, *Bartonia* and *Obolaria*, are saprophytic, but the presence of no small amount of chlorophyll in stems, leaves, and ovaries excludes them from the Holosaprophytes; they may, however, be regarded as Hemisaprophytes. *Bartonia* and *Obolaria* are near allies so far as concerns the imbricated corolla-lobes and the ovules covering the inner face of the carpels ; but the presence of nectaries in the corolla of *Obolaria,* besides the calyx with only two leaves, which resemble bracts, make the genus very distinct from *Bartonia.* Whether these distinctions may prove sufficient for the removal of *Obolaria* from the Erythraeinae we must leave to the judgement of future monographers of the family. In the present paper we wished only to describe the structural peculiarities as a contribution to the knowledge of these peculiar and interesting plants, which, so far, have been only imperfectly known.

EXPLANATION OF FIGURES IN PLATES XXXIII AND XXXIV.

Illustrating Mr. Holm's paper on *Bartonia.*

(The letters in the figures indicate as follows: *Ep.*, epidermis; *End.*, endodermis; *L.*, leptome; *L**., inner leptome; *H.*, hadrome; *M.*, mestome-parenchyma; *P.*, pith.)

PLATE XXXIII.

Fig. 1. Three specimens of *Bartonia verna*; natural size.
Fig. 2. Same species; corolla laid open. × 2.
Fig. 3. Same species; a stamen. × 6.
Fig. 4. Same species; the capsule. × 6.
Fig. 5. A small specimen of *B. lanceolata*; natural size.
Fig. 6. Same species; inflorescence of a larger specimen; natural size.
Fig. 7. Same species; corolla laid open. × 6.
Fig. 8. Same species; a stamen. × 18.
Fig. 9. Same species; a flower. × 4.
Fig. 10. Same species; two capsules, closed and opened. × 6.
Fig. 11. *B. verna*; cross-section of part of stem. × 360.
Fig. 12. Same species; cross-section of part of stem. × 480.
Fig. 13. Same species; cross-section of part of stem, showing a very small collateral mestome-bundle. × 480.
Fig. 14. *B. lanceolata*; cross-section of peduncle, showing a stoma. × 480.
Fig. 15. Same species; cross-section of peduncle. × 600.
Fig. 16. Same species; cross-section of leaf. × 480.
Fig. 17. *B. tenella*; a flower. × 4.
Fig. 18. Same species; corolla laid open; anthers have dropped. × 5.
Fig. 19. Same species; capsule. × 5.

PLATE XXXIV.

Fig. 20. *B. verna*; cross-section of stem. × 480.
Fig. 21. *B. lanceolata*; stoma from the stem. × 360.
Fig. 22. Same species; cross-section of basal internode of stem. × 480.
Fig. 23. *B. verna*; stomata from the stem. × 360.
Fig. 24. Same species; cross-section of one of the higher internodes from about the middle of the stem. × 480.

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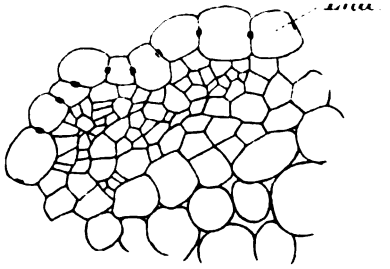
6.



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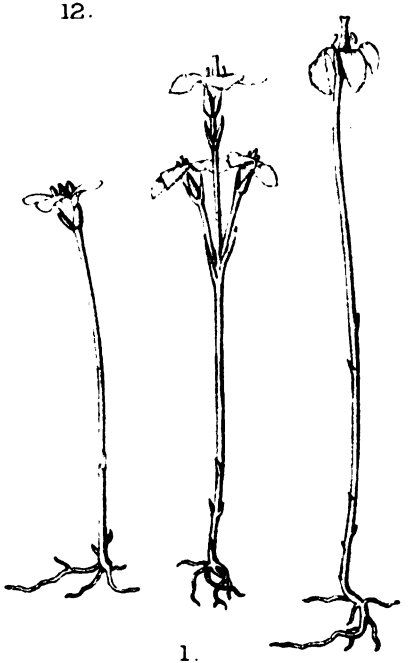

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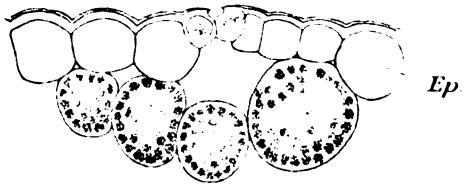

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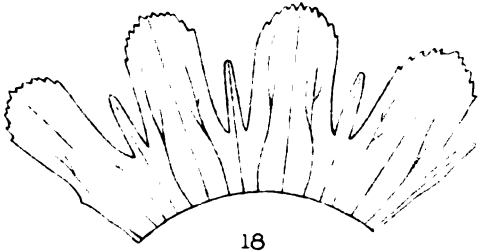

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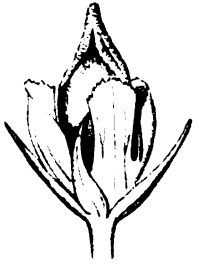

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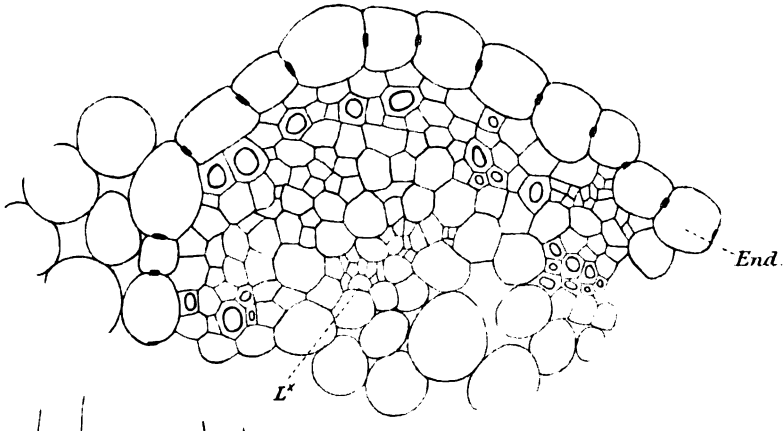
HOLM — BARTONIA.



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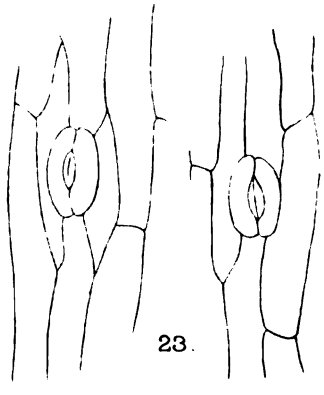

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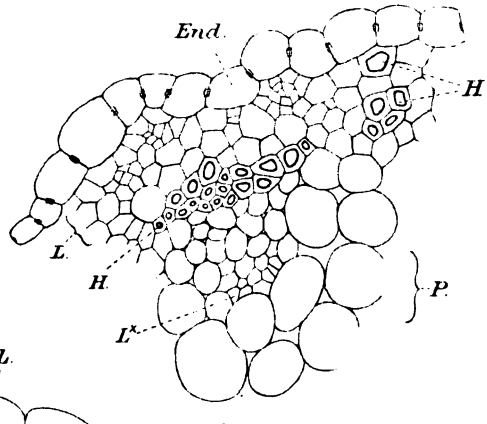

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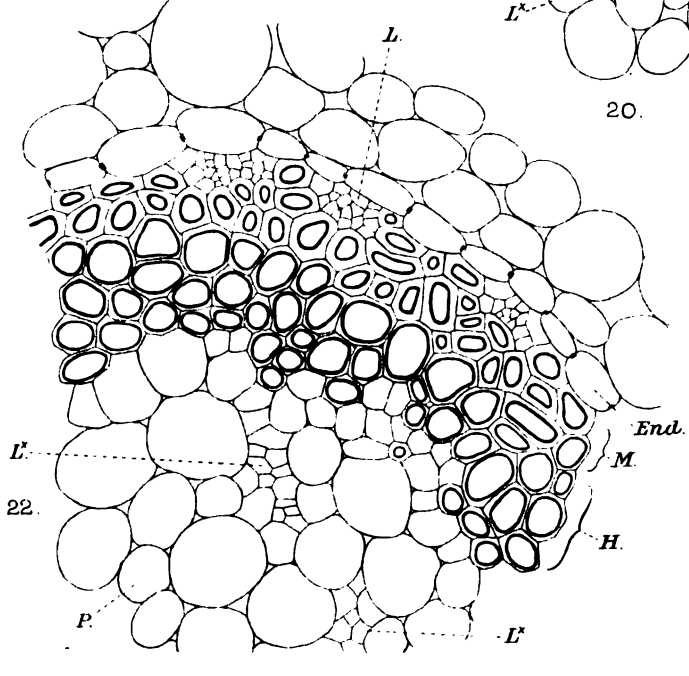

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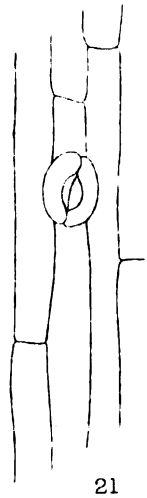

21

Studies of Irritability in Plants [1].

BY

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The Formative Influence of Light.

With Plate XXXV.

1. INTRODUCTION.

As my experiments were abruptly terminated by the earthquake of April 18, it seems on some accounts desirable to record and partly to discuss the results I already have, rather than wait until I can report more. These experiments have been repeated, most of them many times, always with the same results, and I shall go on in the lines which this paper suggests as soon as circumstances permit. The statements of fact I make with no hesitation; the interpretation of these facts I offer subject to such modification as my further work may make necessary. Yet I cannot help feeling that I have gone far enough to justify positive conclusions so far as two species of plants are concerned, and to suggest the reasonableness of the inference that the conditions are not fundamentally different with a considerable number of others.

In 1898 Czapek [2] reported: 'Wenn man Brutkörper von *Marchantia* auf feuchtem Substrat am Lichte . . . auf dem Klinostaten auskeimen lässt, so entstehen im Laufe von 2–3 Monaten kleine schwächliche Pflänzchen, welche aus röhrig zusammengeschlossenen Thalluslappen bestehen, und rings Wurzeln tragen . . . Dieser interessante Versuch

[1] The first paper in this series—Studies of Irritability in Algae, Botanical Gazette, 40, Nov., 1905—was published by Miss Flora A. Randolph and myself. The work of the present paper has been done either by myself alone or, under my direction, by two students, Miss Cora A. Snyder and Miss Clara A. Tompkins. I assume the responsibility for what I here say, however, for I cannot submit this paper to my sometime collaborators, and I have carried the work further than either of them knows. I wish also to acknowledge the careful help of Mr. R. M. Holman, now Assistant in Botany in this University.

[2] Czapek, F., Weitere Beiträge z. Kenntniss der geotropischen Reizbewegungen. Jahrb. f. w. Bot., xxii, 261, 1898.

[Annals of Botany, Vol. XX. No. LXXX. October, 1906.]

lässt sich leider nicht über 2–3 Monate hinaus fortsetzen, weil die Pflänzchen auf einer kleinen Anheftungsstelle senkrecht auf dem Substrate aufsitzend naturgemäss schlecht mit Wasser und mineralischen Nährsalzen versorgt werden, und auch die Befestigung eine mangelhafte ist. Es lasst sich aber doch erweisen, dass die Dorsiventralität auf dem Klinostaten nicht zu Stande kommt.'

This interesting experiment, in which the very marked and long-known dorsi-ventrality of *Marchantia* failed to appear, suggested to me that possibly less imperfect plants, with the same radial structure, might be developed if, instead of beginning with multicellular and comparatively large reproductive bodies like gemmae, spores were used. Furthermore, gemmae are subject to the influence of light, mainly from one direction, during the course of their development on the surface of the thallus. Spores are also more or less illuminated, but only through the surrounding tissues of the sporophyte. Gemmae must develop at once, if at all, and there is no possibility of allowing the effect, if there be any, of light to pass off before they are sown. Spores can be kept for weeks or months in perfect darkness, and the following experiments will show that, in most cases at least, there is not the slightest evidence that they are permanently influenced by the light which filters through overlying tissues upon them.

Although *Marchantia* grows and fruits in the mountains not far from here, it is not easily accessible, and does not fruit at a season when one can conveniently sow the spores. That the spores may be kept as long as other Liverworts growing in dryer places I doubt. These other Liverworts—for example, *Fimbriaria Californica* (*Asterella*), and species of *Anthoceros*, &c.—and such Ferns as *Gymnogramme triangularis*, are abundant, and their spores may be collected in quantity, and sown when convenient.

The great difficulty is in getting clinostats. A good clinostat is expensive, and few American laboratories can afford more than one or two good ones. Following Ganong's directions[1], I had ten eight-day clocks, of the alarm-clock shape but without alarms, cut down so that they ran at four times the speed, removed the hands, and put flat plates on the minute-hand spindles. These clocks therefore give cultures a revolution completed every fifteen minutes. In addition to these eight-day clocks, I had twelve one-day clocks ('dollar clocks'), similarly fitted with plates carried on the minute-hand spindles. These clocks complete in one hour the revolution of a culture carried on the plate. By using clocks of these two speeds, I was led to believe that had Czapek used a faster clinostat he would have succeeded in getting, not folded, but solid cylindrical plants. I will discuss this point later, however. The mere mechanical labour of winding twelve clocks every day, and twenty-two clocks every other day

[1] Ganong, W. F., A laboratory course in Plant Physiology, pp. 120–1, New York, 1901.

for nine months, is tiresome, and I shall in the future use one motive power for as many cultures as possible. Furthermore, no spring clock is absolutely reliable, and though these cheap clocks have served me well enough to enable me to reach certain results, they are not suitable for experiments lasting months at a time. I have lost many cultures because clocks have suddenly stopped which had carried them regularly for months. The loss of time from this cause is often very great. I am now working on a motor which I hope will be both efficient and reliable, and at the same time require less frequent winding.

I began my experiments on Liverworts and Ferns by using small flower-pot saucers of soft porous red clay. These, when used in pairs (the upper saucer containing soil, the lower filled with water), have the great advantage of furnishing well-drained culture dishes. On the other hand, being opaque, they cast a shadow over a greater or less proportion of the surface of the culture. For this reason, I have now used for some time crystallizing dishes of thin white glass, about eight centimetres in diameter and three and a half centimetres deep, covered with the lids or bottoms of Petri dishes. These lids, not fitting tightly, permit fair ventilation, at the same time that they exclude dust and retain moisture. Dull black paper is finally glued over the tops of the lids, so that all light falls nearly or quite horizontally.

The soil used came from the surface of the banks where the Liverworts and Ferns grew from which I collected the spores. The soil was air-dried, freed from pebbles, pulverized in a mortar, and filled into the dishes to the depth of about a centimetre. The soil was moistened from the start with boiled distilled water only, for I wished to avoid an accumulation of salts from our hard tap-water in these undrained dishes. I have not attempted to supply equal quantities of water to the cultures, though I have taken pains to give no excess, and to water fairly uniformly. When the antheridia and archegonia of *Anthoceros* and *Gymnogramme* were ripe, I watered abundantly once or twice, and, a few days after, poured off the excess. Thus I ensured swimming room for the antherozoids, and presently the sporophytes of both began to appear.

In experiments on *Anthoceros* two sets of cultures were used, on sterilized and on unsterilized soil, for both species of *Anthoceros* common here (*A. fusiformis*, Aust., and *A. Pearsoni*, M. A. Howe) contain colonies of *Nostoc* (*sp.*?). I have elsewhere reported[1], however, that *Anthoceros* appears to grow better, and in other respects perfectly normally, without *Nostoc*, and for this reason it is quite fair to use only sterilized soil. The dishes, containing the duly moistened soil and covered, were sterilized on three successive days in an Arnold steam sterilizer, the last sterilization lasting several hours. Though subsequent fungous infections cannot

[1] Peirce, G. J., Anthoceros and its Nostoc colonies, Bot. Gazette, xlii, July, 1906.

always be avoided, and though there may be other spores introduced than those designed, such sterilization as this is efficient in destroying whatever was in the soil and the water at the start.

As I wished to study the early stages in germination, I made a few cultures under somewhat different conditions. I placed a sheet of white filter paper over the moist soil before sterilizing, and afterwards enclosed the dishes in dull opaque black paper except for a slit on one side, one centimetre square, and reaching upwards from the top of the layer of soil. Thus whatever light entered these dishes entered from one direction only, with the rays mainly parallel.

In another case I used Knop's solution, sterilizing as before, placing an equal number of cultures on clinostats and on the shelves beside them.

While in Naples in 1904 I began experimenting similarly with marine algae, and I have had no opportunity as yet to resume experimental work on sea-weeds, though I hope to do so presently. I will report such results as I obtained for whatever suggestive value they may have.

Uniform sowing of spores on prepared surfaces—soil, paper, or water—is not easy, and as the young plants growing up close together shade each other, it is very important that the spores be sown sparingly, and be as uniformly distributed as possible. I have tried to dust them carefully from paper held at some distance above the dishes. By turning the dishes at the same time, some degree of uniformity in distribution is attainable, especially if only a small quantity of spores be used for each dish.

By using dishes no deeper than the crystallizing dishes described, it is possible to place them on the stage of an ordinary microscope, and to examine them without in any way disturbing the cultures. It is necessary to make the camera drawings of clinostat cultures as rapidly as possible, to avoid too long exposure to light from one direction only. The exposure to the comparatively dry air of the laboratory for such short times, say five minutes, seems not to injure the plants, for I have taken pains not to keep the cultures very wet. Where it is necessary to make more careful or more detailed drawings, the only thing to do is to remove the little plant to be studied from the culture altogether, and this means its loss; but I have made many rapid drawings in succeeding weeks of the same plants as they were growing, and in this way I have been able to follow the development of the same individuals.

The cultures were all on shelves in windows facing south-west. Direct sunshine was avoided by window-shades of thin white holland, drawn up from below when needed. The temperature of the laboratory naturally ranged somewhat higher than that out of doors; but it was, nevertheless, not so high by day as that of most American laboratories, artificially heated in winter, and at night it was not so low as out of doors. The result this year was a much more rapid and luxuriant growth in my cultures than

out of doors. This was due largely to the dry and cold November and December, during which out-of-door plants grew but little.

2. THE INFLUENCE OF LIGHT UPON GERMINATION AND EARLY GROWTH.

The germination of the spores of various archegoniates has been repeatedly described in monographs and in larger works[1], and the development of these plants has been studied by many plant physiologists, but I was interested to compare the early stages of germination and growth, with reference to the influence of light, with the behaviour of germinating algal spores, as described by Rosenvinge, Winkler, and myself[2]. To do so, I sowed the spores of *A. fusiformis*, *Fimbriaria Californica*, and *Gymnogramme triangularis*, which I had collected when ripe during the season of 1905, on white filter-paper over damp soil, in covered crystallizing dishes enclosed in black paper. On the side next the window I cut a hole 1 centimetre square in the black paper. The sowing was on March 29. On April 12 I found the first young plants of *A. fusiformis*, two weeks after sowing. These are shown in Pl. XXXV, Fig. 1. The arrow indicates the direction of light. In this culture the sowing was not uniform, and there was more or less shading of adjacent spores by each other; yet, with the apparent but not real exception of the two plants *a* and *b*, which were shaded (the shading neighbour of *a* is not shown), all were not only growing toward the light, but their first division walls were, like those of the algae previously referred to, at right angles to the incident rays. We have here, then, photaxis of the germ-tube, and the determination of the angle of division by the direction of illumination. The influence of light on germination is indicated by the fact that at 3 centimetres away from the opening in the black paper there were no germinations; at 2·4 centimetres, one; at 2 centimetres there were ten; at 1·5 centimetres, twenty-five; and from there on there were too many to count. From this statement, and from Fig. 1, we see, in the first place, that germination itself is dependent upon a certain though undetermined amount of light; and, in the second place, that the direction of growth, and of the successive cell divisions, is determined by the direction of light.

Fig. 2 represents a *Fimbriaria* spore germinating thirteen days after sowing, the arrow, as before, indicating the direction of the incident light. This figure shows that the direction of growth of the germ-tube and of the first division walls is determined by the direction of the light. It may be objected that the division walls are laid down at right angles to the long axis of the germ-tube, and not at right angles to the incident rays. This

[1] For example Campbell, D. H., Mosses and Ferns, 2nd edition, 1905.

[2] Rosenvinge, L. K., Influence d'agents extérieurs sur l'organisation polaire et dorsiventrale des plantes, Revue génér. de Bot., i, 1889. Winkler, H., Einfluss äusserer Factoren auf die Theilung der Eier von *Cystoseira barbata*, Ber. d. Deutsch. Bot. Ges., xviii, 1900. Peirce and Randolph, loc. cit.

is true; but it is the direction of the light that determines the direction of the long axis of the germ-tube. By so doing it affects the plane of division, indirectly if not directly. In any case, it is extremely probable that what appears to be very directly the result of light action, is rather the end result of a long series of reactions, only the first one of which was due directly to the influence of light.

In Fig. 3 is shown a group of two *Fimbriaria* spores, as they were at 2.15 p.m. on the thirteenth day after sowing. The rhizoid formed by one of the little plants had grown out from the side of the plantlet away from the light, and was already bending toward the darker part of the culture. The same plantlets at 11.15 a.m. the next day are shown in Fig. 4. At this time the rhizoid was growing still more markedly away from the light, in spite of the fact that for more than half of the time which had intervened between the two sketches the plants were in darkness, or in extremely feeble light. Fig. 5 shows a plantlet, in which the third and fourth division walls, as well as the first and second, are nearly at right angles to the direction of light. The opaque spore shut off a certain amount of light, and hence the direction of the first wall, parallel with the general direction of the rays, is really at right angles to the rays actually reaching the germ-tube. The figure shows, furthermore, that the rhizoid, as in sessile algae, develops on the darker side.

Although in many cases—in fact, the majority—the spore puts out the germ-tube on the side toward the light, it does not invariably do so. Perhaps this is due to the effect of light upon the spore as it matured in the tissues of the sporophyte. But the spores which send out a germ-tube in other directions than toward the light are relatively so few that I cannot believe this to be the case. Perhaps there is such a thing as polarity in these spores, but, if so, the manner of collecting and sowing the spores should result in a much more general distribution of their poles; their germ-tubes should not originate mainly on any one side, whether toward the light or in any other direction.

Fig. 6 indicates the direction of growth and division of the germ-tubes of *Gymnogramme*, the spores of which I had sown on February 23, and which had been almost continuously illuminated by incandescent electric lights for five weeks. The slowness of germination may have been due to various causes; but the most evident of the possible influences affecting germination was the intensity of the light. For twenty-five days I lighted the cultures by 4-candle power bulbs. Finding such slight evidence of germination at this time, I changed to 8-candle power frosted bulbs, and at the end of three days to 16-candle power clear bulbs. At the end of six days very many fern spores were germinating. The temperature in the box in which lights and cultures were, was about that of the room for the first twenty-five days, and went up to about 32° C. when

I put in the 16-candle power lights. This may have accelerated germination; but the experiment, except as indicating that the direction of growth and of cell-divisions in the germ-tubes of this Fern is influenced by light, even of composition so different from sunlight, was of little value. A repetition of the experiment was interrupted by the earthquake of April 18.

It is conceivable that in all of these cases the side from which the spore puts out the germ-tube, the direction of growth of the germ-tube, and the side of it on which the first rhizoid appears, may be the sides or the direction most free from the mechanical pressure or resistance of particles of soil or of raised spots in the filter-paper on which the spores were sown. To avoid this objection, I sowed spores of *Gymnogramme* on the surface of a filtered Knop's solution in two covered crystallizing dishes. Black paper was glued to the covers, so that light reached the spores only through the sides of the dishes. One dish I placed on a clock-clinostat, making a complete revolution every quarter-hour; the other dish was on the shelf three inches above. Fig. 7 shows two young Ferns, sixteen days after the spores were sown in the dish on the shelf. The light fell in the direction indicated by the arrows. The germ-tubes are growing toward the window, the first division walls are at right angles to the incident rays, and the rhizoids appear on the dark side of the young plants. Fig. 8 is a diagram in which is indicated by arrows the direction of the germ-tubes of the spores germinating on the Knop's solution in the dish upon the clinostat. The age is the same, all the conditions were the same for the two cultures except that in this culture the light entered through all sides successively as the dish was revolved. The direction of growth of the rhizoids was as various as that of the germ-tubes, generally, however, opposite to that of the germ-tube. These two cultures show plainly, therefore, that it is the direction of illumination, and not any mechanical resistance, which determines the direction of growth of the germ-tube and of the first divisions of its cells, and that ordinarily the rhizoids spring from the shaded side of a plantlet, and grow away from the light.

Thus we see that, in respect to their relations to light as an influence directing growth, the spores of these archegoniates behave similarly to the spores of the algae previously described. The advantage is obvious: the germ-tube grows where light will enable the young plant to make food for itself; the rhizoid grows where it can form an attachment for the young plant. At this stage at least, water and food materials are absorbed through all parts of the plant-body; the main function of the rhizoid is to fasten the plant to the soil, and, by giving it suitable mechanical support, enable it to continue the growth of the green parts in the most advantageous direction. This is probably the main function of the rhizoid throughout the lifetime of these small plants; but it may not be the sole function.

3. Description of the Influence of the Direction of Light upon Form.

Spores of *Anthoceros fusiformis* were sown on damp soil in the black-topped crystallizing dishes previously described, some on clinostats, some on the shelf a few inches above them. The sowings were made on November 1. The clinostats made a complete revolution once in fifteen minutes, and were constantly in motion, by night as well as by day. The laboratory was dark between sunset and sunrise. Seven weeks, less one day, after sowing I made the drawing reproduced as Fig. 9. This represents a young plant taken out of the culture and placed in part profile in a drop of water on a slide. The general shape of the plant is that of a vase, with a flaring concave top, lobed in outline, borne on a solid base tapering to the bottom. From all sides of the base rhizoids grow in various directions. The soil on which this plant grew was not sterilized, and the plant contained one *Nostoc* colony of normal size and appearance. If this figure be compared with Figs. 10 and 10*a*, representing a plant growing in a dish on the shelf immediately above the clinostat, but otherwise under as nearly as possible identical conditions, it becomes evident that there are decided differences. Fig. 10*a* is an optical section of the plant drawn from above in Fig. 10. These drawings show a lobed plant expanded at right angles to the light (the arrow indicates the direction from which the light comes) and bearing rhizoids on the shaded side only. This is the usual form of the ordinary young plant of *A. fusiformis* whether grown in culture or found out of doors. The position of the plant is unusual in one respect; it is nearly vertical to the surface of the soil instead of being more or less closely appressed to it. The reason is that the light falls upon the culture in a direction nearly parallel to the surface of the soil, whereas out of doors the light usually falls at nearly a right angle to the surface. The position of the plants out of doors and in cultures is the same in relation to the light—the dominant influence—namely at right angles to it. The direction of the surface of the soil exerts no influence on the direction of growth except as it ordinarily determines the direction from which the light comes.

Corresponding with the results indicated by the foregoing figures of *A. fusiformis* are the results of sowings of spores of *A. Pearsoni*, one set in dishes revolving on clocks and the other in dishes unmoved on the shelf three inches above. Figs. 11 and 11*a* show plants six weeks, less one day, after sowing. The clock was a slow one, making a complete revolution once an hour. In spite of this rate of revolution, one quarter as fast as that of the clock carrying the plant of *A. fusiformis* shown in Fig. 9, these plants of *A. Pearsoni* (Fig. 11) are solid, conical, not rolled or flat, flaring and lobed at the top, and having rhizoids all around their cylindrical bases. The little plant from a culture on the shelf and shown in Fig. 11*a* is in very

sharp contrast to these, being flat and expanded at right angles to the incident rays of light, and having rhizoids on the shaded side only.

Similar cultures of *Fimbriaria Californica* are shown in Figs. 12 and 12*a*. Fig. 12 shows plants growing on a quick clock, revolving completely four times an hour, and drawn five weeks and one day after sowing. These plants are solid, erect, with conical more or less lobed and concave tops borne on cylindrical bases, from all sides of which rhizoids spring. Fig. 12*a* shows a shelf plant of the same age, with the ordinary form, expanding at right angles to the light, and with rhizoids only on the shaded side. Fig. 13 shows a plant midway between Figs. 12 and 12*a* in form. This plant grew on a slow clock, making only one revolution per hour. The plant was drawn five weeks and a half after sowing. The plant is going over from the vasiform to the usual flattened thallus. This change is completed a little later. Indeed on all my clocks, fast or slow, *Fimbriaria* plants lose their early cylindrical form sooner or later. Whether grown on clocks or shelves these plants are all cylindrical at first. The only difference made by my clocks is to defer the period of flattening. The clocks defer this for a longer or shorter time according to their speed, the faster the clock the more perfectly round the plant and the longer it will remain so. I have as yet no means of revolving cultures more rapidly than four times an hour, but I hope to have on resuming these experiments next September.

Cultures of *Gymnogramme triangularis* five weeks and a day after sowing are shown in Figs. 14 and 14*a*. Although spores were sown in a culture on a quick clock, the young prothalli of this fern did not remain cylindrical in form beyond the very early filamentous stage. I shall try this again, however, when I have the means of more rapidly revolving cultures, and also of exposing stationary cultures to equal illumination on all sides. Figs. 14 and 14*a* show plainly, however, that the light determines which side of the thallus shall develop rhizoids, and where the illumination is approximately equal on all sides rhizoids develop on the various sides of different prothalli. Fig. 15 shows a prothallus seven weeks after sowing on a slow clock. The prothallus is thin and expanded, though its edges are somewhat rolled, and it bears approximately equal numbers of rhizoids on its two faces. Furthermore, antheridia and archegonia develop equally on the two sides. It is perfectly possible to suppress the development of the reproductive organs of this fern by insufficient light, but when the illumination is approximately equal and is sufficient on all sides, the antheridia and archegonia develop in spite of there being no shaded side. The advantage of their developing on the shaded, usually the lower, side is evident, but the reason for their doing so is far from clear when it is possible, as just stated, to suppress their formation altogether by feeble illumination.

For one reason or another, the final and most compelling being the earth-

quake of April 18, I have so far been prevented from carrying cylindrical plants of *Anthoceros fusiformis* to the fruiting stage. The spores sown earliest, on September 14, 1905, were sown on slow clocks, making a complete revolution only once an hour. These clocks at first ran somewhat irregularly, stopping at times, and consequently spoiling my cultures and necessitating restarting them. More dependable means of revolving cultures than cheap clocks I expect to have in the autumn. I will record, however, that the sporophytes of this species of *Anthoceros* began to be of visible size about five months after sowing in cultures on the shelf. This shows that, though *Anthoceros* usually holds over from season to season, it can fruit during the first season from the spore, provided the rains come early enough and the winter is wet and warm enough. *Fimbriaria*, on the other hand, did not reach the reproductive stage in my cultures during this season, and probably requires two seasons in which to mature sufficiently to reproduce itself. Of this last I am by no means certain, however, and I shall watch the results of future experiments to determine this point.

Fig. 16 is a drawing of a plant of *A. fusiformis* nine weeks after sowing on a clock revolving the culture once an hour. This plant is drawn from above, and though presenting in general a circular outline, it is bilaterally rather than radially symmetrical. It is like those plants of *Fimbriaria* previously described which, growing on slow clocks, resemble both the shelf plants and those growing on faster clocks.

It is evident that only those unshaded plants near the centre of even small culture dishes, such as I have described, receive an equal amount of light from all directions. Only these plants can be expected to be and are radially symmetrical. Between the centre and the outer edge of each clock-culture the young plants are decreasingly cylindrical, increasingly dorsiventral, and those on the edge are of the usual out of door or shelf form. Furthermore, it is now especially evident why it is so important that spores must be sown sparingly; the young plants must be as remote and as nearly equidistant from each other as possible to avoid shading. Plants shaded on one side by a neighbour even near the centre of cultures on the quicker clocks are as dorsiventral as plants on the shelves. The results of equal illumination on all sides are clear and certain in all cultures of *Anthoceros*, but it is necessary to notice carefully that the illumination is equal for any particular plant under observation. Remote from the centre of a clock culture, or shaded by too close neighbours, or even on a slow clock, the illumination is not equal on all sides. *Anthoceros* appears to be less sensitive, or it reacts more promptly, than the other Archegoniates used in these experiments. This, however, I shall presently discuss.

As stated in the introduction, I have but begun experimenting on the question of the influence of the direction of light upon the form of sea-weeds,

but I will here record the results yielded by an experiment made during a two months' stay at the Zoological Station in Naples[1]. Spores of *Dictyopteris polypodioides* were allowed to escape in sea-water in crystallizing dishes, the covers of which had sheets of black paper glued upon them. Two of these dishes were put on clock works which revolved them once an hour in a horizontal plane. The others were placed on the window shelf beside them. These spores develop at first protonema-like filaments, as Reinke showed[2], on which, during the first two weeks, erect and conical buds appear. At the end of two weeks or so a flat plate begins to grow from near the top of these little balloon-like buds. This is what ordinarily happens in shelf cultures, and is presumably what happens in the sea. Fig. 17 shows the usual young plant. On the other hand in clock cultures the course of events is decidedly different, as shown by Fig. 17*a*. This figure was drawn from a plant at the centre of a dish on a clock, the spores being sown twenty-three days before the drawing was made. It is evident that no part of the plants had become flat, although branching had occurred. Fig. 17 indicates that, under ordinary illumination from one side only, the young plant soon sends out a branch which, growing upward, is thin, flat, and leaf-like.

Certain species of *Fucus*, common between the tide-marks on rocky portions of this coast, are flat and expanded. Spores of these species germinate in dishes of sea-water in the laboratory, as I know by experience. As soon as possible I shall try to cultivate these on clocks and on the shelf, and I hope to follow the experiment which promised such interesting results but which was cut short by the brevity of my stay in Naples. I record the experiment here merely because the preliminary result is so consistent with the results of my experiments on land-plants, not because I think it conclusive or more than suggestive and promising.

4. Discussion of the Influence of Light upon Form.

The results previously described show that certain dorsiventral Archegoniates and one marine alga are more or less influenced as to their form by the direction from which the light falls upon them as they grow. This influence is most evident in the case of *Anthoceros*, which, whether growing on a slow clock or on one which revolves four times as fast, develops with radial instead of dorsiventral structure. All of the plants

[1] The main results of my work are reported in the paper on Irritability in Algae previously referred to. In that paper I took occasion to express my grateful appreciation of the opportunity of working at one of the tables supported at the Zoological Station by the Carnegie Institution of Washington. I am glad to have this additional opportunity to thank the officers of both institutions for their help and courtesy.

[2] Reinke, F., Entwickelungsgeschichtliche Untersuchungen über die Dictyotaceen des Golfes von Neapel, Nova Acta Leopold. Acad., 1, 1878.

experimented upon are positively phototropic, growing erect on the clocks and toward the light in the shelf-cultures. But, as *Anthoceros* shows, we can distinguish between the directive and the formative influence of light. It is also possible to discriminate between the influence of the *direction* from which the light comes, which, in a way, moulds the shape of an organism, and the influence of the quantity or intensity of light, which affects both the quantity and the kind of growth. Thus cultures too feebly illuminated contain thin, long, slender plants ('drawn,' as a horticulturist might say), which do not develop reproductive organs, though the plants may be large enough. Light, then, is a necessary stimulus to the formation of archegonia and antheridia, and light sufficient for vigorous vegetative growth may not be sufficient to stimulate plants to form reproductive organs. This, Vöchting [1], Klebs [2], and their followers have shown. But given the necessary quantity or intensity of light [3], its direction will profoundly affect the form of a growing plant, and also the positions of the vegetative and other organs which develop upon it. This is evidently true of *Anthoceros*, but is not by any means so evident in the cases of *Fimbriaria* and *Gymnogramme*. Why? To answer this question we must examine the actual working of our clinostats. Unless cultures are constantly and uniformly illuminated, the plants do not receive at all times equal amounts of light on all sides. Thus, the gradually increasing light at dawn finally becomes sufficiently strong to exert a definitely stimulating influence upon the plants on which it falls. The plants are in a certain position when the light attains this degree of intensity. The revolving culture will bring them successively into all other possible positions, until finally, at the end of a quarter-hour or of an hour, according to the speed of each particular clock, they come once more into the position in which they were first stimulated by the light. The time of revolution, whether a quarter-hour or even an hour, may or may not be less than the time requisite to exert a lasting influence upon the form of the young plants. But in the morning the stimulus exerted upon any one part is followed by an equal, or even greater, stimulus exerted upon all other parts in succession, thus balancing effects on opposite sides. This is not the case at sunset. As the light fades, there comes a moment when the light still definitely stimulates a growing part, but, the moment after, the light does not stimulate the part presented to it by the revolving clock. And so it goes the night through, and till dawn again. The part last stimulated can react unopposed or unbalanced by other parts. However, if the clocks be sufficiently fast, and although the part last stimulated

[1] Vöchting, H., Über den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüthen, Jahrb. f. wiss. Bot., xxv, 1893.

[2] Klebs, G., Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen, Jena, 1896.

[3] For a voluminous discussion of this topic see Mac Dougal's Influence of Light and Darkness on Growth and Development, Mem. N. Y. Bot. Gard. II, New York, 1903.

has been stimulated once more than any other part of the plant, there will be no visible evidence of this; the plant will be radial in structure, cylindrical or vase-like in form, as my *Anthoceros* cultures show.

This result implies two things: *first*, that the plants do not react very promptly to single stimuli; and, *second*, that the rate of revolution of the clinostat is such that no part of the plant remains exposed so long to the light that the stimulus and the reaction of any one part will not be equalled on and by all other parts. Both these conditions are realized in my cultures of *Anthoceros*, but not with the other two Archegoniates. The thalli of *Fimbriaria* and the prothalli of *Gymnogramme*, grown from the spore on clocks, are as dorsiventral as in shelf-cultures. This may be because the plants owe their dorsiventrality to something else than the influence of light; *or*, because they are more sensitive, or react more promptly to single stimuli than *Anthoceros*: *or*, because at sunset the last stimulus is sufficient to induce and fix dorsiventrality before the morning light can balance this influence.

As is well known, since Pfeffer's work on *Marchantia*[1], dorsiventrality once induced cannot be reversed. Nor is it possible to convert one of these dorsiventral plants into a radial one[2], though the change from the radial to the usual dorsiventral structure may be promptly made. Clinostats revolving faster than any which I have so far employed may show which of these possibilities is the fact, or it may be necessary to use constant approximately equal illumination from all sides. The former can be arranged, and I hope to have such experiments going by autumn. Experiments with electric lights were already in progress, and these will be resumed presently; so I hope to be able to report that, with due attention to details, experiments on these plants yield results similar to those which I have described above for two species of *Anthoceros*.

In speaking of the induction of dorsiventrality in the Marchantiaceae, Pfeffer[3] says: 'Im näheren ist dann immer noch zu entscheiden, ob die Dorsiventralität sich auch bei allseitig gleicher Beleuchtung ausbildet, ob also die einseitige Beleuchtung nur räumlich orientirend wirkt, oder ob sie eine unerlässliche Bedingung für die Entstehung der Dorsiventralität ist. Letzteres scheint nach Versuchen von Czapek bei *Marchantia* der Fall zu sein, da sich aus der Brutknospe bei allseitig gleicher Beleuchtung (auf dem Klinostaten) im Laufe von 2–3 Monaten kleine schwächliche Pflänzchen von radiärem Bau entwickelten. Aus diesen Erfahrungen würde zugleich folgen, dass in diesem Falle, wie es zu erwarten ist, das Zustandekommen der Dorsiventralität eine Bedingung für eine kräftige Entwickelung ist.'

[1] Pfeffer, W., Symmetrie und specifische Wachsthumsursachen, Arb. d. bot. Inst. Würzburg, i, 1891. [2] Czapek, loc. cit.

[3] Pfeffer, W., Handbuch der Pflanzenphysiologie, Bd. II, i, p. 182, 1904.

As I have shown above, equal illumination is not perfectly attained by the use of the clinostat alone. Illumination, to be equalized by a clinostat, must also be constant. This, sunlight is not. Artificial lights may be used night and day, but their composition is not altogether like that of sunlight. The use of artificial light, which I have begun, involves the question of which rays are the more potent in influencing the forms of plants. To this question I shall give attention. But, so far as my experiments have gone, it seems that the usual dorsiventrality of *Anthoceros* may be replaced by a remarkably regular radial structure whenever the light is made to fall, even in approximately equal strength, on all sides successively. If *Anthoceros* plants, started under equal illumination from the spore, can be made to grow at all in darkness, their behaviour will be very significant. If they become dorsiventral under these conditions, it would seem that the tendency to become dorsiventral is inherited, and was held in check only by abnormal illumination. If they continue to be radial and yet grow, it would seem that dorsiventrality is not inherited, but is induced by certain conditions, and it would also seem that a certain factor in the environment, the light and its direction, constitute this condition. To determine whether light from one side only is a condition merely, or is a necessary stimulus to dorsiventrality, is more difficult. This question can be answered by employing suitable artificial lights, perhaps incandescent electric bulbs of equal candle power, and so disposing them that cultures are equally lighted on opposite sides by two or by four lights. If with equal illumination on two opposite sides, the young plants are dorsiventral, Pfeffer's suggestion[1]—that 'lighting from one side is a condition necessary for the development of dorsiventrality'—would seem superfluous, and that the light acts rather as a definite stimulus, the direction from which the light comes being also significant. These experiments had also been begun, but had yielded no definite results before the earthquake stopped my work.

The significance of such an investigation as this, the early results of which I have reported in the foregoing pages, consists not merely in the matters of fact thus revealed, but also in the light these facts throw on the problem of heredity. Every biologist is driven sooner or later to a contemplation of one aspect or another of this problem. The continuity of substance from parent to offspring constitutes, according to most persons, so very much the principal basis of heredity that it may almost be called the sole one in their estimation. Such biologists attempt to express in morphological or in other definite terms the means of transmitting characters from one generation to the next. Thus by chromosomes or germ-plasm or some other name the part or parts are designated to which especial importance

[1] Loc. cit.

is attributed. Or others, attempting to reduce the process to greater precision, would designate in terms of still smaller units—namely the chemical compounds concerned—the means of continuance of bodily characters. But since a chemical reaction depends upon the substances employed and also upon the conditions prevailing at the time, it is only where like substances act upon each other under like conditions that the results are alike. It is therefore as important to study the conditions of life as its physical basis in order to understand the phenomena of life. Analytic and experimental study of the environment will enable us, in the course of time, to reduce to definite terms of physics, as well as of chemistry, much of what is now indefinitely summed up under the name of heredity. We shall see that, along with continuity of substance, the continuity of influence must be reckoned as indispensable to heredity; that, indeed, the continuity of influence is part, and a large part, of heredity.

I have shown in the foregoing pages that, according as the direction of illumination is usual or unusual, certain plants have their normal form or some other wholly different. Whether we regard illumination from only one direction as merely a condition or as a direct stimulus to the development of dorsiventrality in *Anthoceros*, it is evident that, unless the young plants developing from the spore are exposed to influences like those under which their parents developed, they will be unlike their parents. So far as two species of plants are concerned I have furnished experimental evidence in favour of the hypothesis previously advanced [1] that, in addition to what is actually transmitted from parents to offspring in the continuity of substance, the likeness of parents and offspring is due to the likeness (or identity) of influence to which succeeding generations are exposed. In other words, certain physical factors of the environment, constant or periodic but unchanging, constitute means of repeating parental characters generation after generation, and these environmental influences are as essential as the substance. Given the same chemical compounds and the same arrangement of these in the fertilized egg as in the parents, the young must be like the parents *if* their environment is the same. But if any factor vary—in the chemical composition or in the structure of the fertilized egg, or in the conditions under which the young develop—the young will be proportionally different from the parents. The individual young will differ not only from their parents but also from each other. We are accustomed to these differences among the individuals of a brood. We are in the habit of thinking of the environment as introducing variety. The changing factors of the environment do introduce variety. So do the changing compounds or proportions of compounds in the bodies of the parents and in the fertilized eggs which

[1] Farmer, J. B., On stimulus and mechanism as factors in organization, The New Phytologist, ii, Nov. and Dec., 1903. Peirce, G. J., Text-book of Plant Physiology, pp. 279–83, May, 1903; Certain undetermined factors in heredity and environment, Amer. Naturalist, xxxviii, April 1904.

are the fruit of their bodies. Yet there are unchanging factors in the environment. These also contribute to the repetition of parental characters in the offspring. A knowledge of these definite forces, which we can recognize and the effects of which we can study, will help us to solve the problem of heredity.

STANFORD UNIVERSITY, CALIFORNIA.
June, 1906.

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EXPLANATION OF FIGURES IN PLATE XXXV.

Illustrating Professor Peirce's Paper on Irritability in Plants.

Fig. 1. *Anthoceros fusiformis*. Spores germinating fourteen days after sowing, light only from direction of arrow. × 84.

Note direction of growth of germ-tube. Plants *a* and *b* shaded by others.

Fig. 2. *Fimbriaria Californica*. Spores germinating thirteen days after sowing, light only from direction of arrow. × 84.

Note directions of germ-tube, cross-walls, and rhizoid.

Fig. 3. *Fimbriaria Californica*. Group of two spores at 2.15 P.M., thirteen days after sowing, light only from direction of arrow. × 84.

Fig. 4. *Fimbriaria Californica*. Same group of two spores twenty-one hours later. × 84.

Fig. 5. *Fimbriaria Californica.* Germinating spore, fourteen days after sowing. × 84.
Note directions of growth and of cross-walls.

Fig. 6. *Gymnogramme triangularis.* Spores germinating under constant electric light, almost five weeks after sowing, light only from direction of arrow. × 300.
Note directions of growth of germ-tubes and of cross-walls.

Fig. 7. *Gymnogramme triangularis.* Spores germinating on Knop's solution sixteen days after sowing, light from direction of arrow. × 300.
Note directions of germ-tubes, rhizoids, and cross-walls.

Fig. 8. *Gymnogramme triangularis.* Diagram showing directions of rhizoids of young plants sixteen days after sowing on Knop's solution revolved on clinostat. × 70.

Fig. 9. *A. fusiformis.* Young plant almost seven weeks after sowing on ¼ hour clinostat revolving culture of unsterilized soil. × 41.

Fig. 10. *A. fusiformis.* Young plant of same date ot sowing, culture receiving light from direction of arrow. × 41.

Fig. 10 *a. A. fusiformis.* Optical section of plant shown in Fig. 10. × 41.
Compare radial form of Fig. 9 and dorsiventrality of Figs. 10 and 10 *a.*

Fig. 11. *A. Pearsoni.* Young plants just over six weeks after sowing on one hour clinostat revolving culture of sterilized soil. × 41.

Fig. 11 *a. A. Pearsoni.* Young plant of same date of sowing, culture receiving light from direction of arrow. × 41.
Compare this with Fig. 11 as to form.

Fig. 12. *Fimbriaria.* Young plants almost five weeks after sowing on ¼ hour clinostat. × 41.

Fig. 12 *a. Fimbriaria.* Young plant of same date of sowing, culture lighted from direction of arrow. × 41.

Fig. 13. *Fimbriaria.* Young plant 5½ weeks after sowing on one hour clinostat, going over to dorsiventral form. × 41.

Fig. 14. *Gymnogramme.* Prothalli almost five weeks after sowing on ¼ hour clinostat. × 41.

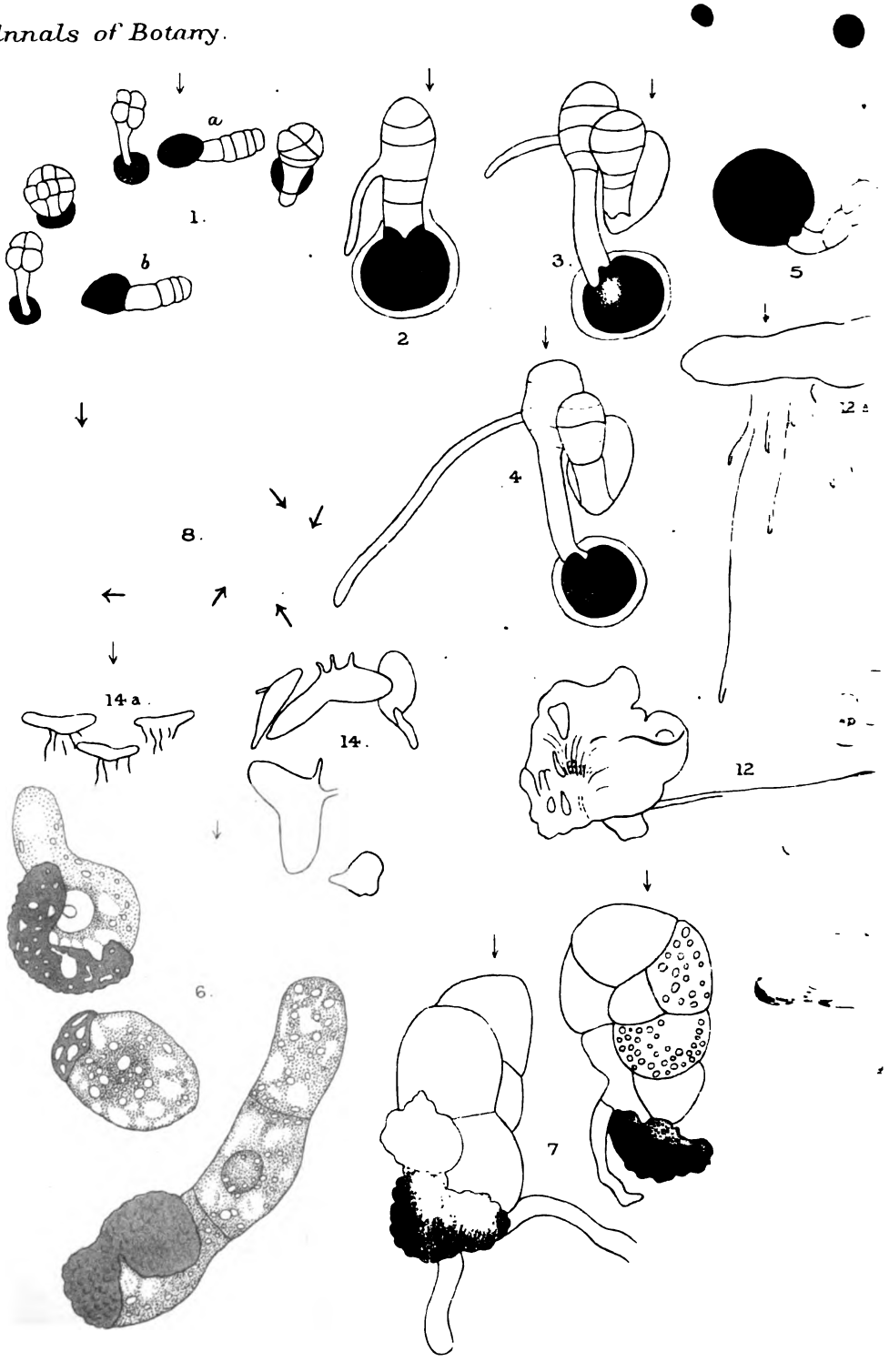
Fig. 14 *a. Gymnogramme.* Prothalli of same date of sowing, culture receiving light from direction of arrow. × 41.

Fig. 15. *Gymnogramme.* Prothallus seven weeks after sowing on one hour clinostat. × 41.
Rhizoids and reproductive organs on both sides.

Fig. 16. *A. fusiformis.* Young plant almost nine weeks after sowing on one hour clinostat. × 41.
Note half-round form on slow clock.

Fig. 17. *Dictyopteris polypodioides.* Young plant in dish of sea-water on shelf, receiving light from one side only. × 125.

Fig. 17 *a. Dictyopteris polypodioides.* Young plant twenty-three days after sowing in sea-water on one hour clinostat. × 125.



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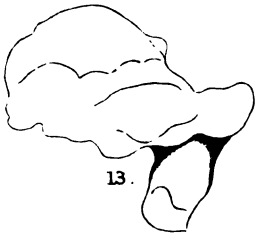
PEIRCE – FORMATIVE INFLUENCE OF LIGHT.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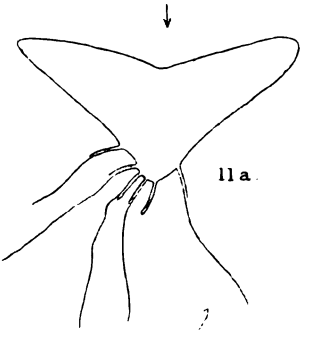
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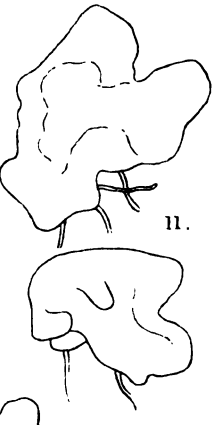
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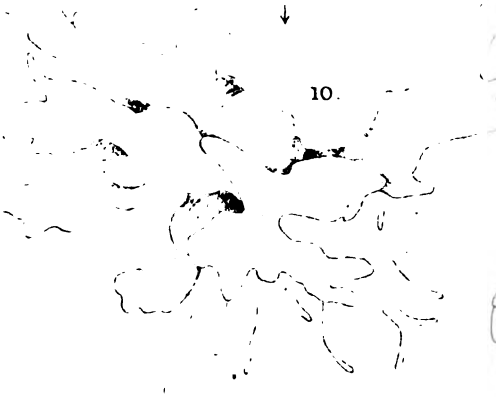
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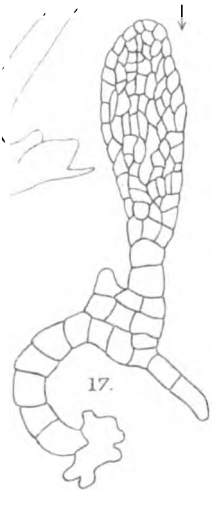
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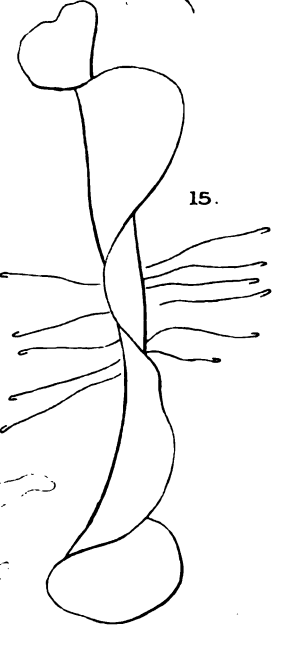
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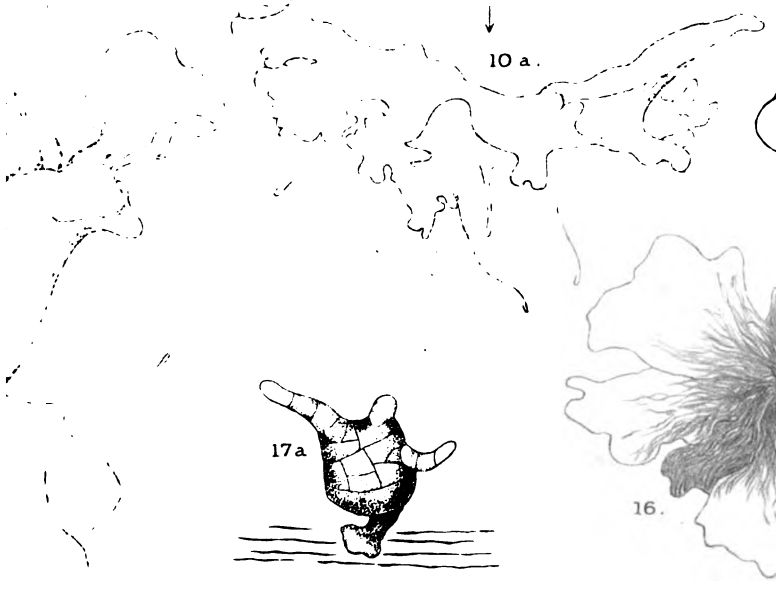
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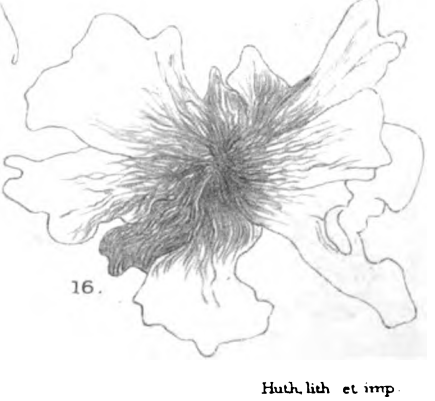
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NOTES.

ON THE JULIANIACEAE, A NEW NATURAL ORDER OF PLANTS. (Abstract.)[1]—I. General Description. The Julianiaceae comprise, so far as at present known, two genera and five species. They are resiniferous, tortuously branched, deciduous, dioecious shrubs or small trees, having alternate, exstipulate, imparipinnate leaves, from about one to three decimetres long, clustered at the tips of the flowering branches and scattered along the short barren shoots. The flowers are small, green or yellow-green, quite inconspicuous, and the males are very different from the females. The male inflorescence is a more or less densely branched axillary panicle or compound catkin, from 2½ to 15 cm. long, with weak, thread-like, hairy branches and pedicels. The male flowers are numerous, 3 to 5 mm. in diameter and consist of a simple, very thin perianth, divided nearly to the base into four to nine narrow equal segments, and an equal number of stamens alternating with the segments. In structure and appearance they are almost exactly like those of the common oak. The female inflorescence is similar in structure to that of the sweet chestnut, consisting of an almost closed, usually five-toothed involucre, borne on a flattened pedicel and containing three or four collateral flowers, of which the two outside ones are, perhaps, always abortive.

At the flowering stage, the female inflorescences including the narrow flattened pedicel and the exserted styles, are about 2 cm. long, and, as they are seated close in the axils of the crowded leaves and of the same colour, they are easily overlooked. The female flowers are destitute of a perianth, and consist of a flattened, one-celled ovary, terminated by a trifid style and containing a solitary ovule. The ovule in both genera is a very peculiar structure. I will first describe that of *Juliania*. In the flowering stage it is a thin, flat, obliquely horseshoe-shaped or unequally two-lobed body, about 2 mm. in its greatest diameter, attached to the base of the cell. At a little later stage, in consequence of unequal growth, it is horizontally oblong, nearly as large as the mature seed, that is 6 to 8 mm. long, and almost symmetrically two-lobed at the top. A vascular bundle or strand runs from the point of attachment to the placenta upwards near the margin into one of the lobes. In this lobe the embryo is tardily developed, and at this stage it is more or less enclosed in the opposite lobe, the relations of the two being as nozzle and socket to each other. It is assumed that the whole of this body, with the exception of the lobe in which the embryo is formed, is a funicle with a unilaterally developed appendage, which breaks up and is absorbed during the development of the ovule into seed. A similar growth and transformation is unknown to me in any other natural order.

[1] Read before the Royal Society on June 28, 1906.

The ovule of *Orthopterygium* is very imperfectly known, but the attachment appears to be lateral and the funicular appendage cup-shaped at the basal end, bilamellate upwards, and more or less enclosing the embryoniferous lobe.

Mr. Boodle, who has fully examined the ovule of *Juliania* from microtome sections, describes it as hemianatropous with a single integument.

The compound fruits of *Juliania* are samaroid in form, the wing being the flattened pedicel, at the base of which it disarticulates from the undifferentiated part of the pedicel. They vary from 4 to 7 cm. in length by 1½ to 2½ cm. in width. Externally they strongly resemble the samaroid pods of certain genera of Leguminosae, notably those of *Platypodium* and *Myroxylon*. The involucre itself, of the largest fruits seen, is only about 1 cm. deep by 2 cm. wide. It is composed of very hard tissues and is quite indehiscent. Only quite young fruit of *Orthopterygium* is known. In this the flattened pedicel is narrow, straight and aequilateral, from 6 to 7 cm. long and about 1 cm. wide.

The nuts of *Juliania* are almost orbicular, biconvex, hairy on the outside and have a very hard endocarp. The solitary exalbuminous seed is circular or oblong, 6 to 10 mm. long, compressed, with a smooth, thin testa. The embryo is horizontal, with thin plano-convex, more or less oblique, obscurely lobed cotyledons, which are epigaeous in germination, and a long ascending radicle applied to the edges of the cotyledons.

II. History. It is surprising that a genus of plants so striking in aspect, so distinct in the shape of its fruit, and so widely spread as *Juliania* is in Mexico, should have entirely escaped the observation of all the earlier European travellers in that country.

C. J. W. Schiede, M.D., who accompanied Ferdinand Deppe on a botanical expedition to Mexico in 1828, was apparently the first to send dried specimens to Europe of one of the species of *Juliania*. But it was not until 1843 that his friend, Dr. D. F. L. von Schlechtendal, published an account of the genus of plants in question.

Under the name of *Hypopterygium* (subsequently *Juliania*) *adstringens*, he very fully described the material he had an opportunity of examining, but he had neither female flowers nor mature seeds, and he was doubtful whether the fruit was the result of one or more flowers. His description is very accurate, and he expresses his views of the affinities of the plant, which he regarded as a type of a new Natural Order. Since Schlechtendal's time, until I took up the study of the genus five years ago, nobody seems to have had sufficient material to supplement his description.

In 1854, A. Gray described, also from very incomplete material, what he considered a second species of the same genus, collected in Peru. An examination of fuller, though by no means complete, material has led me to separate it generically under the name of *Orthopterygium*.

In September, 1900, the late Mr. Marc Micheli presented Kew with a small set of E. Langlassé's Mexican plants. Among them was a specimen in fruit, which, after much research, was identified with Schlechtendal's *Juliania adstringens*; but the most careful and tedious examination carried me no further than Schlechtendal had reached sixty years before. Previous to this (in 1899, as I afterwards found out), Kew

received a specimen of a male plant collected in the Mexican State of Jalisco by Mr. C. G. Pringle, n. 6871, and doubtingly named *Juliania adstringens*.

The male specimen was published as *Juliania mollis*, Hemsl., and the fruiting as *J. adstringens*, Schl.

This publication had the desired effect, for it brought me a letter at the end of 1901 from Dr. J. N. Rose, Curator in the 'Division of Plants' of the United States National Museum at Washington, from which I make the following extracts:—

'You will also be interested in what I have to tell you about *Juliania*. For more than six years I have been at work off and on, at this genus, but for the lack of material I have never published anything upon it, but each time have brought back specimens, and this year was especially fortunate in collecting near the type-locality both male and female plants. In looking up the subject since my return I find that you have anticipated me and have published two very beautiful plates and some interesting notes. . . . There are, however, more than two species in Mexico. I have certainly four well-marked species and possibly six. . . . With regard to the position of this genus, I think it must be regarded as the type of a new order. I do not think it has any relationship to either Burseraceae or Anarcardiaceae. My conclusions in the field were that it must be closely related to Juglandaceae, a relationship which you also suggest.'

In this communication Dr. Rose most generously offered to send all his specimens and notes to me, leaving it to my judgement in what form publication should be effected. I gladly accepted, and through the kindness of the Trustees of the Bentham Fund, Miss M. Smith made an elaborate series of drawings under my direction. As there were still some structural points on which we were not quite clear, and Dr. Rose contemplated another visit to Mexico, it was decided to publish at once a description of the genus, as then understood, and brief diagnoses of the species.

III. Geographical Distribution. 1. *Juliania*.—So far as at present known *Juliania* is confined to Mexico, and the various species occur in isolated localities between about 17° 40′ and 23° N. lat., and 97° and 104° W. long., and at altitudes of about 1,500 to 5,500 feet.

2. *Orthopterygium*.—The habitat of the Peruvian *Orthopterygium Huaucui* is 2,000 miles distant from the nearest locality of any species of *Juliania*. The exact position of the only place in which it has been found cannot be given, but it is in the Province of Canta, in the Department of Lima, between 11° and 12° S. lat.

IV. The Affinities of the Julianiaceae. During the six years that I have had this small group under observation I have had opportunities of showing the specimens and drawings to many of the leading botanists of the world, and all agree who have seen them that it deserves to rank as an independent order. That being so, the question of its position arises, but that is a point not so easily settled in a linear arrangement. Taking the morphological characters seriatim, it is evident that the closest relationships are with the Anacardiaceae and Cupuliferae. The absolute separation of the sexes and the very great diversity of the floral structure of the sexes, associated with pinnate leaves, offer a combination of characters probably without a parallel.

Beginning with the foliage, the Julianiaceae have alternate, exstipulate, impari-

pinnate leaves in common with at least eight different ligneous orders, but here the affinity, or, rather, resemblance ends so far as six of them are concerned, and the comparisons need be carried no further. There remain the Anacardiaceae and Juglandaceae, both of which are also resiniferous, both have unisexual flowers with reduced envelopes, at least as to some of their members, and both have solitary, exalbuminous seeds. Other points of resemblance or similarity in the Juglandaceae are the dissimilar male and female flowers, the broad, stigmatic lobes of the style, and the single-coated ovules. *Juglans* has also a funicle of unusual development. But the combined characters in common of the Julianiaceae and the Juglandaceae cannot be regarded as constituting a close affinity. In some respects there is a nearer relationship to the Anacardiaceae. The anatomical characters of the two orders are very much alike; but as Dr. F. E. Fritsch will describe and discuss the anatomy in a separate paper, it is unnecessary to enter into particulars here.

The nearest approach I have found to the singular funicular development of the ovule is in the Anacardiaceae, but the resemblance is remote and the ovules of the latter are double coated. Coming to the seed and the embryo, however, the resemblance is complete, and, apart from the slight obliquity of the cotyledons of *Juliania*, the description of the seed and embryo of *Cotinus* or *Rhus* would do for *Juliania*. With this the affinities to the Anacardiaceae are exhausted, and they are not sufficiently strong to justify the juxtaposition of the two orders. The next comparison is with the Cupuliferae, taking the order as limited by Bentham and Hooker. There is nothing in the secretions nor in the foliage to warrant an approximation of the two orders, and in habit of growth the Julianiaceae are very different. But divergences as great, or greater, exist between closely associated orders, and even between genera referred to the same order; and when we come to the inflorescence and flowers, affinities are evident; that is if affinities are deducible from similarities in structure.

The male inflorescence, the male flowers, and the pollen of *Juliania adstringens* are so near in texture, structure, and form to the same parts in certain species of oak that, detached, they might be referred to the genus *Quercus*. In fact, there is much greater dissimilarity in the male inflorescence and flowers of different species of *Quercus* than there is between those of *Juliania* and those species of *Quercus* which have a flaccid male inflorescence and stamens alternating with the segments of the perianth.

The female inflorescence and the male flowers of *Juliania* are not represented by exact counterparts in the Cupuliferae, but the analogies are perhaps greater than with any other order. Several female flowers in a closed involucre is a characteristic of *Juliania*, of *Fagus*, *Castanea*, and *Castanopsis*. In all three of the genera of the Cupuliferae named, the involucre dehisces regularly or irregularly, and the nuts fall out. In *Juliania* the involucre is indehiscent, and the flattened nuts are adnate by their edges to the inner wall of the involucre, and they have a very hard, relatively thick, sclerenchymatous pericarp.

Going back to the flowers, the male of *Juliania* has a perianth; the female, none. In *Corylus* the conditions are reversed; in *Betula*, neither sex has an obvious perianth; in *Quercus*, the flowers of both sexes are furnished with a perianth.

All of the Cupuliferae have an ovary which is more than one-celled, and usually

there are three cells, and mostly more than one ovule in each cell, though each nut is usually only one-seeded. The ovary of *Juliania* and of *Orthopterygium* invariably contains only one ovule. The flowers and nuts of *Castanea* are collateral, as in *Juliania*. The seeds of both orders are exalbuminous, and the cotyledons are epigaeous in germination.

Weighing the characters in which there is agreement or similarity between the Julianiaceae and the Anacardiaceae, and those in which there is agreement or similarity between the Julianiaceae and the Cupuliferae, the latter in my estimation preponderate; and I cannot suggest a more natural position for the Julianiaceae, in a linear arrangement, than between the Juglandaceae and the Cupuliferae.

W. BOTTING HEMSLEY.

HERBARIUM, ROYAL BOTANIC GARDENS, KEW.

ON THE SEEDLING STRUCTURE OF GYMNOSPERMS[1]. *Taxus baccata.*—The two cotyledons each contain a single collateral bundle, which is, in some cases, slightly mesarch. A section of the axis, taken through the cotyledonary node, shows the central region to be occupied by six plumular bundles arranged in two groups. Each seed-leaf-trace, at its entry into the hypocotyl, has its xylem arranged in a V-like manner, the protoxylem being near the apex, which is pointed outwards. Each cotyledonary bundle travels obliquely downwards, and during its passage the phloem is resolved into two parts. At the same time the metaxylem passes in more quickly than the protoxylem, so that the latter, for a time, is entirely mesarch in position. The phloem masses of the cotyledon bundle fuse with the corresponding tissue of the nearest plumular bundle—the three strands of each group having fused together—and, concurrently, the metaxylem of the same traces moves towards the xylem of the epicotyledonary bundles; hence the protoxylems of the seed-leaves are left in a more exarch position, and, ultimately, are quite exposed. The vascular tissues close up and become more compact, thus a typical diarch root results. It is not possible to distinguish any rotation of the protoxylem: it ultimately occupies an exarch position, because it is left isolated by the movements of the metaxylem. There may be made out, however, an indefinite rearrangement of the protoxylem, coupled with a slight centrifugal movement, after the exarch position has been attained.

Taxus cuspidata, as far as can be ascertained from the study of old seedlings, does not differ in any essential feature from the above species.

Cephalotaxus pedunculata is very similar to *Taxus*. The main points of difference are as follows: (*a*) The single bundle of each cotyledon shows the mesarch structure more highly developed; and (*b*) the seed-leaf-traces do not bifurcate so soon. They enter the central region of the axis as well-defined collateral endarch structures, and form a cylinder with the plumular traces, the phloem forming a practically closed

[1] Abstract of paper read before Section K at the York meeting of the British Association, August, 1906.

ring. At a lower level, the bast-circle divides, opposite the cotyledon bundles, into two well-defined masses. During this rearrangement the xylem groups come into contact, the metaxylem derived from the seed-leaves joins up with the plumular xylem, and thus the protoxylem becomes isolated. The subsequent changes are essentially the same as those described for *Taxus*.

Cupressus pisifera, *C. Lawsoniana*, and *Thuja orientalis* all have two cotyledons, each with a single collateral vascular bundle. The transition phenomena are of the same type as in *Taxus*, and result in the formation of a diarch root.

Libocedrus decurrens, also, is similar, but the number of seed-leaves is three, and the primary root is triarch.

Cedrus Deodara.—There are usually eleven or twelve cotyledons; the number, however, varies. Each contains a single collateral endarch bundle throughout its whole length.

Above the cotyledonary node the seed-leaves fuse to form a well-defined tube, the inner surface of which is corrugated; each ridge corresponds to a cotyledon, the foliage leaves of the first node fit into the furrows, and, before the axis is reached, these leaves fuse with the cotyledonary tube. Fusion with the axis takes place, and the general appearance of a transverse section, taken immediately below the cotyledonary node, is that of a monocotyledonous stem. This appearance is, of course, due to the disposition of the leaf-traces of the first three or four nodes; these bundles, however, speedily lose their identity, and, a little later, so also do the vascular strands of the first node. The bundles of the cotyledons now become placed closely together, so that the limits of any one is difficult to determine. At a lower level a gradual change occurs; the phloem groups fuse together in pairs, and, at the same time, the masses of xylem undergo rotation in such a manner that two neighbouring protoxylems become exarch, fuse, and occupy positions alternating with those taken up by the phloem groups. Thus a typical root is formed, usually pentarch or tetrarch.

Abies Firma, *Actinostrobus*, *Callitris*, *Larix*, and some species of *Pinus*, are, on the whole, of the same type.

Pinus Murrayana var. *Sargenti*.—Four cotyledons are usually present: each contains a single bundle which has transfusion tracheids adjoining.

Near the base of the cotyledons the phloem of the bundles bifurcates, and the xylem rotates in such a manner that the protoxylem becomes situated between the two groups of phloem elements. In this condition they enter the axis, and in their passage towards the centre the rearrangement becomes more marked. During the downward course the eight phloem groups fuse in pairs, the metaxylem takes up a position internal to the phloem, and, as the protoxylem is already exarch, a tetrarch root is formed.

There is, however, some variation. Thus another seedling also had four cotyledons, the bundles of three of which exhibited the rearrangement described above while still in the leaf, while the fourth remained undivided throughout its whole course. The central region of the axis being reached, the fourth cotyledonary bundle played the part of a plumular trace, and fused up with the two epicotyledonary bundles situated upon its flanks. The other three seed-leaf strands behaved in the manner already indicated above. Their phloem groups joined with the adjacent bast

of the plumular bundles, and the same applies to their metaxylem elements. A triarch root was thus formed.

Pinus montana var. *gallica*, *P. sylvestris*, *P. Thunbergii*, *P. Gerardiana*, and others all follow a course similar to the above. There is, however, much variation both in the number of the seed-leaves and also in the behaviour of the bundles of the cotyledons.

Tsuga diversifolia may be placed in a position intermediate between the *Taxus* and *Pinus* types.

CONCLUSIONS.

1. A mesarch structure is exhibited in the cotyledonary bundles of *Cephalotaxus*, *Taxus*, and possibly other plants.

2. The Gymnosperms, as a whole, conform to Van Tieghem's type 3 of rotation; there are, however, three varieties of this type: (1), that in which the bundle of the cotyledon is endarch throughout, and the rotation of the protoxylem very indefinite, e.g. *Cephalotaxus*; (2), that in which the seed-leaf-trace is endarch but the rotation of the protoxylem takes place in the hypocotyl, e.g. *Cedrus*; and (3), that in which the rotation of xylem and bifurcation of the phloem of the cotyledonary bundle take place in the seed-leaf, e.g. *Pinus*.

These varieties merge one into the other; it is not possible to draw a definite line of demarcation between them.

3. The numerous cotyledons obtaining in many plants have been formed by the splitting of pre-existing ones. This conclusion is based on the results obtained from the study of many individuals of species with a varying number of seed-leaves.

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ON THE SEEDLING STRUCTURE OF CERTAIN CENTROSPERMAE[1].—NYCTAGINACEAE: *Allionia albida*, Walt.—The petiole of each cotyledon contains a central strand, consisting only of a very few tracheae, derived from one of the bundles of the midrib, and bounded on each side by two normal collateral bundles, the smaller ones being outermost. Near the base of the petiole the traces *a* fuse with the larger bundles *b*. The axis, at the level of the cotyledonary node, contains six plumular strands, which soon fuse together to form two. On the arrival of the seed-leaf bundles into the central cylinder, the groups of tracheae *c* 1 and *c* 2 occupy their isolated positions between the bundles *b* 1, *b* 2, and *b* 3, *b* 4 respectively; while *b* 2, *b* 4, and *b* 1, *b* 3 are separated by the plumular traces *d* 2 and *d* 1 respectively.

Following the hypocotyl downwards, the relations between the bundles are somewhat complicated. *c* 1 and *c* 2 occupy their position throughout, but there is much anastomosing between the bundles of the series *b* and *d*. At the same time the protoxylems of *b* 2, *b* 4, and *b* 1, *b* 3 rotate towards *d* 2 and *d* 1 respectively. This rotation is, however, vacillating, and the rearrangement arrived at may be obliterated

[1] Abstract of paper read before Section K at the York meeting of the British Association, August, 1906.

by the formation of a branch passing from *b* 3 to *d* 1, for example. Finally, however, the branching stops, the strands *d* 1 and *d* 2 having combined with one of the bundles situated on their flanks, and a definite rotation of the protoxylems *b* 2, *b* 4, and *b* 1, *b* 3 takes place. The condition now obtaining is that of a tetrarch root; this last movement, however, is too late, for almost immediately the phloem and metaxylem of *b* 2, *b* 4, and *b* 1, *b* 3 fuse together, enclosing in their meshes the exarch protoxylem which was derived from these same bundles. Thus the groups of tracheids *c* 1 and *c* 2, which have been gradually increasing in number, form the protoxylem of the diarch root.

Mirabilis divaricata, Lowe, follows a similar course.

AMARANTACEAE: *Amaranthus hypochondriacus*, L.—Each cotyledon has a single bundle. Bifurcation of the phloëm and the rotation of the xylem towards the exarch position commence some way up the petiole. On the central region of the axis being reached, the rotation of the xylem is seen to be complete, the metaxylem elements speedily pass inwards and, at a lower level, the opposing masses of phloem fuse together. A diarch root is thus formed.

The same changes occur in *A. caudatus*, L.

The transition-phenomena in all the following plants are essentially of the same nature as in *Amaranthus*:—

AIZOACEAE: *Tetragonia expansa*, MURR., *Mesembryanthemum crystallinum*, L.

CARYOPHYLLACEAE: *Corrigiola litoralis*, L., *Lychnis Viscaria*, L., *Polycarpon tetraphyllum*, L., *Silene Otites*, Sm., and *Silene pendula*, L.

PORTULACACEAE: *Portulaca oleracea*, L., *Calandrinia Menziesii*, TORR. et GRAY.

CHENOPODIACEAE: *Atriplex hastata*, L., *Chenopodium Bonus-Henricus*, L., *Spinachia oleracea*, L.

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